Laura del Rio-Hortega Balsalobre

Understanding selectivity on the prokaryotic microbiome in Larger Benthic Foraminifera

UNIVERSIDADE DO ALGARVE

Faculdade de Ciências e Tecnologia

2023

Laura del Rio-Hortega Balsalobre

Understanding selectivity on the prokaryotic microbiome in Larger Benthic Foraminifera

Mestrado em Biologia Marinha

Supervisors:
Willem Renema
Co-supervisor
Aschwin H. Engelen

UNIVERSIDADE DO ALGARVE

Faculdade de Ciências e Tecnologia

2023

Declaração de autoria de trabalho

Understanding selectivity on the prokaryotic microbiome in Larger Benthic Foraminifera

Declaro ser a autora deste trabalho, que é original e inédito. Autores e trabalhos consultados estão devidamente citados no texto e constam da listagem de referências incluída

Laura del Rio-Hortega Balsalobre

Copyright em nome de Laura del Rio-Hortega Balsalobre, da Universidade do Algarve.

A Universidade do Algarve reserva para si o direito, em conformidade com o disposto no Código do Direito de Autor e dos Direitos Conexos, de arquivar, reproduzir e publicar a obra, independentemente do meio utilizado, bem como de a divulgar através de repositórios científicos e de admitir a sua cópia e distribuição para fins meramente educacionais ou de investigação e não comerciais, conquanto seja dado o devido crédito ao autor e editor respetivos.

Acknowledgments

This work would not have been possible without Prof. Willem Renema and Elsa Girard, which gave me the opportunity to be part of their research team, as well as for always being available during the development of my master thesis. I would also like to thank Aschwin Engelen and Rita Castilho for their time and support. Finally, I would like to thank my parents for helping me follow my career choices, my loved ones and myself for pursuing this work.

RESUMO

As interações simbióticas entre microrganismos, tanto procariontes quanto eucariontes, desempenharam um papel significativo na formação do curso da evolução da vida na Terra. Essas relações levaram a estratégias ecológicas engenhosas com impactos de longo alcance nos ecossistemas, como os recifes de coral. Nos recifes de coral, as associações simbióticas são cruciais para manter a saúde geral do recife, com microrganismos estabelecendo conexões próximas com vários organismos, facilitando a troca de compostos e desempenhando papéis essenciais no ciclo de nutrientes.

Um organismo que desempenha um papel fundamental nos ecossistemas de recifes, mas muitas vezes é negligenciado, é o Foraminífero Bêntico Maior (FBM). Os FBM são protistas unicelulares encontrados em ecossistemas costeiros tropicais. Eles contribuem significativamente para o equilíbrio de carbonato do recife através da calcificação, influenciando a estrutura do recife, os sedimentos e o equilíbrio químico. Os FBM demonstraram sensibilidade às condições ambientais, tornando-os indicadores potenciais da condição dos recifes de coral. Eles dependem de relacionamentos simbióticos para crescimento e calcificação, o que tem despertado um interesse crescente no estudo da dinâmica de seu microbioma. Além de seu simbionte eucarionte, é sabido que os FBM também abrigam comunidades procarióticas, embora sua contribuição para o sucesso dos FBM seja muito pouco estudada. Por um lado, uma parceria de longo prazo com procarióticos específicos do hospedeiro sugere a presença de forças ecológicas e evolutivas significativas que promovem e sustentam essas associações. Por outro lado, uma variabilidade no microbioma tem sido proposta como vantajosa, especialmente em resposta a condições em mudança.

Considerando a importância dos Foraminíferos Bênticos Maiores (FBM) na manutenção e preservação dos ecossistemas de recifes, torna-se urgente compreender seu sistema holobionte procariótico. Este estudo tem como objetivo i) comparar o microbioma procariótico dos FBM com os microbiomas da água do mar e do substrato, ii) identificar um potencial microbioma procariótico central específico da espécie e iii) estudar a influência do local na composição do microbioma procariótico.

O estudo concentrou-se nos Foraminíferos Bênticos Maiores (FBM), que são protistas marinhos unicelulares encontrados em águas rasas tropicais e subtropicais. O Arquipélago de Spermonde abriga esses organismos, habitando principalmente substratos como destroços de coral revestidos de algas coralináceas crostosas e áreas arenosas. O Arquipélago de Spermonde, situado próximo a Sulawesi, Indonésia, no coração do Triângulo de Coral. Este arquipélago é composto por aproximadamente 120 ilhas e bancos de recifes, localizados em uma ampla plataforma de carbonato que se estende por 40 km e atinge profundidades de até 60 metros. A área de estudo tem um clima de monção, com uma estação seca de maio a outubro, caracterizada por ventos do sudeste que desencadeiam a ressurgência, e uma estação chuvosa de novembro a abril, marcada pelo aumento da hidrodinâmica e pelas entradas de água doce dos rios, levando a uma redução na salinidade e aumento da turbidez. Tempestades sazonais e ondulações contribuem para a disponibilidade de substrato para colonização de foraminíferos e moldam as condições físico-químicas.

A coleta foi realizada em agosto de 2022 em três locais de duas ilhas habitadas, Badi e Padjenekang, no platô do recife e na encosta do recife. Amostras de água do mar foram coletadas perto do substrato, filtradas e armazenadas para extração de DNA. Amostras de substrato foram coletadas e examinadas sob um microscópio para remover os FBM visíveis, com foco no estudo do microbioma do próprio substrato. A coleta de foraminíferos envolveu a coleta de espécimes do substrato, destroços de coral ou algas. Esses espécimes foram limpos para eliminar microorganismos externos e matéria orgânica, armazenados e posteriormente submetidos à extração de DNA. Foram escolhidas cinco espécies-alvo de foraminíferos para análise com base em características específicas, incluindo a presença de diatomáceas e testes lisos. Essas espécies incluíram *Amphistegina radiata, A. lessonii, A. lobifera, Calcarina spengleri, Heterostegina depressa* e *Neorotalia calcar.*

A extração de DNA foi realizada usando diferentes kits e protocolos para amostras de água do mar, substrato e foraminíferos, e controles negativos foram usados para validação. As regiões variáveis-alvo V4-V5 do gene 16S rRNA foram amplificadas usando os iniciadores 515F-Y e 926R. As Variantes de Sequência Exatas (ESVs) foram sequenciadas usando Novaseq. Essas amplificações foram realizadas por meio de uma reação em cadeia da polimerase (PCR) de duas etapas, primeiro para amplificar a região-alvo 16S e depois para marcar o DNA usando índices duplos exclusivos de 10 pb (UDI) da IDT. Para análise de dados, o estudo utilizou o software R, dependendo principalmente de pacotes como phyloseq e microbiome. Pacotes específicos de análise estatística e visualização foram empregados conforme necessário.

A comparação do microbioma procariótico dos FBM com o do ambiente circundante, incluindo água e substrato, revela insights emocionantes sobre a especificidade e singularidade dessas comunidades microbianas. Contrariamente ao esperado, o microbioma dos FBM é notavelmente distinto tanto da água do mar quanto do substrato. Essa diferenciação é marcada pela compartilhamento muito baixo de ESVs procarióticos dentro dos FBM com seu ambiente, mas também pela ausência de um microbioma central compartilhado entre os FBM em contraste com um microbioma central amplo tanto na água do mar quanto no substrato.

O substrato, onde os FBM residem e se alimentam, era esperado ter uma sobreposição mais substancial na composição microbiana com os FBM. No entanto, a composição distinta do substrato, caracterizada por uma riqueza relativamente baixa de espécies microbianas, mostrou o contrário. Essas descobertas desafiam a noção de uma transferência direta de microrganismos entre os FBM e seu ambiente imediato, enfatizando a complexidade das interações microbianas dos FBM.

Em contraste, a água do mar se destaca como o compartimento mais diverso, abrigando um microbioma central rico e diversificado compartilhado entre ilhas e áreas de recifes. Esse fenômeno pode ser atribuído à alta conectividade do fluxo de água nos ecossistemas de recifes, facilitando o transporte de matéria orgânica e inorgânica, bem como de microrganismos, entre diferentes áreas.

A especificidade de espécie do microbioma procariótico dos FBM é uma descoberta central deste estudo. Cada espécie de FBM hospeda um microbioma procariótico único, sugerindo que as associações microbianas estão intrinsecamente ligadas à identidade da espécie hospedeira. Essa observação está em consonância com pesquisas anteriores que consistentemente identificaram microbiomas distintos dentro das espécies de FBM.

Essas descobertas indicam uma preferência seletiva por espécies microbianas específicas pelos FBM, reforçando ainda mais a noção de uma relação simbiótica.

Curiosamente, apesar do microbioma central específico da espécie, há flexibilidade dentro do microbioma central que varia em diferentes áreas do recife. Essa adaptabilidade sugere a capacidade dos FBM de ajustar suas comunidades microbianas em resposta às condições ambientais em mudança. Essa flexibilidade pode conferir uma vantagem adaptativa, auxiliando no sucesso de colonização dos FBM em vários ecossistemas marinhos ao longo da história geológica. No entanto, uma investigação genética e fisiológica mais aprofundada é necessária para confirmar definitivamente a existência de simbiose entre os FBM e seu microbioma procariótico.

A influência da ilha e da área de recife na composição do microbioma procariótico dos FBM não pode ser subestimada. Variações na composição do substrato entre diferentes ilhas contribuem significativamente para as diferenças nas comunidades microbianas. Os substratos distintos de cada ilha, seja dominado por algas ou areia, desempenham um papel fundamental na formação da diversidade e composição microbiana dentro dos FBM.

Além disso, fatores terrestres, como a presença humana, podem ter um impacto profundo na qualidade da água, o que, por sua vez, afeta a comunidade bacteriana. A baixa qualidade da água, combinada com uma alta entrada de matéria orgânica, tem sido associada a uma maior abundância de classes microbianas específicas, como Gammaproteobacteria, Bacilli e Bacteroidia, que são abundantes no microbioma procariótico dos FBM de uma das ilhas.

Dentro das áreas de recife, são evidentes dissimilaridades nas comunidades microbianas. Embora o compartilhamento de espécies microbianas entre áreas seja limitado, é observado um maior grau de compartilhamento entre espécies de FBM que habitam a mesma área de recife. Variações de profundidade também exercem influência, com espécies de FBM amostradas em diferentes profundidades na mesma área exibindo diferenças em seu microbioma procariótico. A heterogeneidade inerente dos ecossistemas de recifes, onde cada habitat possui suas próprias condições ambientais únicas, desempenha um papel crucial na formação do microbioma procariótico dos FBM.

Em conclusão, este estudo fornece informações valiosas sobre as dinâmicas intrincadas dos microbiomas procarióticos dentro dos Foraminíferos Bênticos Maiores e sua profunda influência nos ecossistemas de recifes. A natureza específica da espécie e dependente do local desses microbiomas procarióticos, distintos do ambiente circundante, destaca a complexidade das interações microbianas dentro dos FBM. A presença de ESVs específicas em indivíduos da mesma espécie sugere a existência de uma relação simbiótica, embora pesquisas adicionais sejam necessárias para uma confirmação definitiva. O impacto da ilha, da área de recife e da composição do substrato nas comunidades microbianas destaca a sensibilidade dos microbiomas dos FBM aos fatores ambientais. Essa sensibilidade pode potencialmente contribuir para a adaptabilidade e o sucesso de colonização dos FBM em diversos ecossistemas marinhos. Essas descobertas aprofundam nossa compreensão da simbiose nos ecossistemas de recifes, enfatizando a necessidade de pesquisa contínua para desvendar as complexidades desses habitats marinhos vitais.

Palavras-chave: Foraminíferos Bentónicos Maiores, microbioma procariótico, *Amphistegina, Calcarina, Heterostegina, Neorotalia*

ABSTRACT

Symbiotic interactions between microorganisms have played a pivotal role in shaping Earth's evolutionary trajectory. Coral reefs, characterized by intricate ecological strategies, are prime examples of the profound influence of these symbiotic relationships on ecosystems. Among the organisms central to coral reef health are the Larger Benthic Foraminifera (LBFs), single-celled protists found in tropical coastal ecosystems, significantly contribute to reef carbonate balance. Although there is an understanding of their eukaryotic microbiome, their prokaryotic microbiomes remain vastly understudied. This study explores the prokaryotic microbiomes of LBFs by i) comparing the LBF prokaryotic microbiome to seawater and substrate microbiomes, ii) identifying a potential species-specific core prokaryotic microbiome, and iii) studying the influence of the site on the prokaryotic microbiome composition. Sampling encompassed LBFs, seawater, and substrate at the Spermonde Archipelago in Indonesia. The target variable regions V4-V5 of the 16S rRNA gene were amplified and the Exact Sequence Variants (ESVs) were sequenced using Novaseq. The results show a big divergence between LBFs' microbiomes and those of their surrounding environment, seawater, and substrate. The species-specificity of LBFs' prokaryotic microbiome was evident, with each LBF having one or two very abundant ESVs and in some cases having a core microbiome. This selectivity suggests a symbiotic relationship between LBFs and specific microbial species, contributing to their adaptability and colonization success across diverse marine environments. The island and reef area exerted substantial influence on microbiome composition. Dissimilarities in microbial communities were observed among reef areas, with LBFs species within the same area exhibiting greater similarity. Depth variations further emphasized the role of environmental heterogeneity in shaping LBFs' prokaryotic microbiome. The ability to have a flexible prokaryotic microbiome have been proposed as advantageous, particularly in response to changing conditions. These findings deepen our understanding of the symbiosis in reef ecosystems, emphasizing the need for continued research to understand the intricacies biotic relationships in reefs.

Key words: Larger Benthic Foraminifera, prokaryotic microbiome, *Amphistegina, Calcarina, Heterostegina, Neorotalia.*

Understanding selectivity on the prokaryotic microbiome in Larger Benthic Foraminifera

Understanding selectivity on the prokaryotic microbiome in Larger Benthic Foraminifera

INTRODUCTION

Symbiotic interactions, encompassing both prokaryotes and eukaryotes microorganisms, have profoundly influenced the course of life evolution on Earth (Archibald, 2015; Margulis, 1971; Sapp, 1994). In a symbiotic relationship, the consortium of microorganisms residing in and on an organism, the host, is known as its microbiome. These relationships have led to ingenious ecological strategies (Goffredi et al., 2005; Lee et al., 2010) with possibly far-reaching impacts, shaping entire ecosystems as coral reefs (Roth, 2014 and references within).

In reefs, symbiotic associations play a key role. Both eukaryotic and prokaryotic microorganisms are crucial to maintaining overall reef health, generating close symbiotic connections with numerous organisms (e.g., Pernice et al., 2020; Rosenberg et al., 2007). These microorganisms are adept at trading various compounds with and are translocated to the host by direct digestion of the symbiont cells (Fankboner, 1971; Titlyanov et al., 1996; Wiedenmann et al., 2023). The symbiotic relationship between microalgae and coral species is well-documented, enabling the survival of corals throughout their evolutionary history (Blackall et al., 2015). Moreover, the microbiome of sponges, an increasingly explored subject, has revealed remarkable diversity (Freeman et al., 2021). However, there is one organism which has a strong relationship with its microbiome and plays a pivotal role in reef ecosystems but it is often overlooked—the Larger Benthic Foraminifera (LBFs).

Larger Benthic Foraminifera are single-celled protists that are prominent in tropical coastal ecosystems. They play a vital role in reef carbonate balance through calcification, accounting for nearly 5% of the annual carbonate production in present-day reef and shelf areas worldwide (Langer, 2008). As a result, LBFs influence the reef structure and sediments as well as help to maintain chemical equilibrium by acting as buffers against pH changes by test (shell) dissolution after their demise (Yamamoto et al., 2012).

LBFs has shown a big sensitivity to the surrounding physicochemical conditions, to the point that they have been put forward as effective indicators of coral reef condition (e.g. Girard et al., 2022; Hallock et al., 2003; Humphreys et al., 2022). Like many marine organisms, LBFs rely on symbiotic relationships for both growth and calcification (Hallock, 1985; Lee, 2006), and their microbiome has shown to have a rapid response to environmental stressors, particularly elevated sea-surface temperatures and water quality (Prazeres, 2018; Schmidt et al., 2011; Webster et al., 2013, 2016). The importance of LBFs in the reef system and their capacity to be an indicator of reef degradation has led to an emerging interest in studying their microbiome dynamics.

To date, the main focus of research on LBFs' microbiome has been directed towards eukaryotic symbiosis in LBFs. However, LBFs also host prokaryotic communities (Bourne et al., 2013; Martin et al., 2019; Prazeres, 2018; Prazeres et al., 2017; Webster et al., 2013, 2016), although this diversity and their contribution to the success of LBFs is very understudied. The few studies available have shown that the prokaryotic community in LBFs is species-specific (Bourne et al., 2013; Martin et al., 2019; Webster et al., 2016) and part of that microbiome is constant across the individuals of the same species (Martin et al., 2019), known as the core microbiome. A long-term partnership with host-specific bacteria, suggests the presence of significant ecological and evolutionary forces that promote and sustain these associations (Ainsworth et al., 2015; Reveillaud et al., 2014). Nonetheless, LBFs have demonstrated the capacity to establish site-specific microbiomes, that can vary across different areas of the same reef (Prazeres et al., 2017). Also, this microbiome can re-assemble when populations encounter diverse environmental conditions (Prazeres, 2018). This variability in the bacterial microbiome has been proposed as advantageous, particularly in response to changing conditions (Ziegler et al., 2017).

Considering the importance of Larger Benthic Foraminifera (LBFs) in maintaining and preserving reef ecosystems, it becomes urgent to comprehend their prokaryotic holobiont system. In this study, next-generation sequencing will be applied to characterise the prokaryotic microbiomes of six LBFs, collected from diverse reef sites spanning two islands within the Spermonde Archipelago (Indonesia). This investigation aims to i) compare it to seawater and substrate microbiomes, ii) identify a potential species-specific core microbiome, and iii) study the influence of the site on the microbiome composition.

METHODS

Study Area

The Spermonde Archipelago (Fig.1A) is located in the heart of the Coral Triangle, near the southwest coast of Sulawesi, Indonesia, within the Makassar Strait. It encompasses around 120 reef islands and shoals, situated on a broad carbonate platform that spans 40 km and reaches a maximum depth of 60m. The cay-crowned reefs and shoals are aligned parallel to the coast, and the reef flat is typically very shallow, with a maximum depth of 0.5m during low tide (for a more detailed description of the reef system, see Renema et al. (2001).

This region experiences a monsoon climate, characterised by a dry season from May to October, dominated by SE winds that trigger upwelling at the outer shelf rim. During the wet season (November to April) the hydrodynamics are at their peak, and the nearshore freshwater inputs are accentuated by the fluvial discharges, primarily from the Jene Berang and Maros rivers. Consequently, this results in reduced salinity, increased amounts of silts, terrigenous sands, and pollutants, ultimately leading to a decrease in light penetration (Erftemeijer, 1993), defining it as a turbid reef system.

In the Spermonde Archipelago, the most common substrates for Larger Benthic Foraminifera (LBFs) are coral rubble coated with crustose coralline algae and sandy areas. Additionally, in certain locations, seasonal storms and swells lead to frequent rubble avalanches, creating vast areas of substrate that are suitable for foraminifera colonisation.

Larger Benthic Foraminifera (LBFs), are a group of marine protists belonging to the phylum Foraminifera. These single-celled organisms are characterized by their large size, complex chambered shells, and benthic (bottom-dwelling) habitat in various marine environments, primarily tropical and subtropical shallow waters. The distribution of LBFs in the Spermonde Archipelago can be found in Renema et al. (2001).

The sampled locations are the two Islands Badi and Padjenekang, both inhabited. Badi is situated in the 30-40m depth area of the platform while Padjenkang is situated in the 20-30m depth area. The sampling sites in Badi had mainly a substrate composed of rubble and macroalgae (Fig. 1B), while in Padjenekang it was mainly a mix of rubble and sand (Fig.1C).

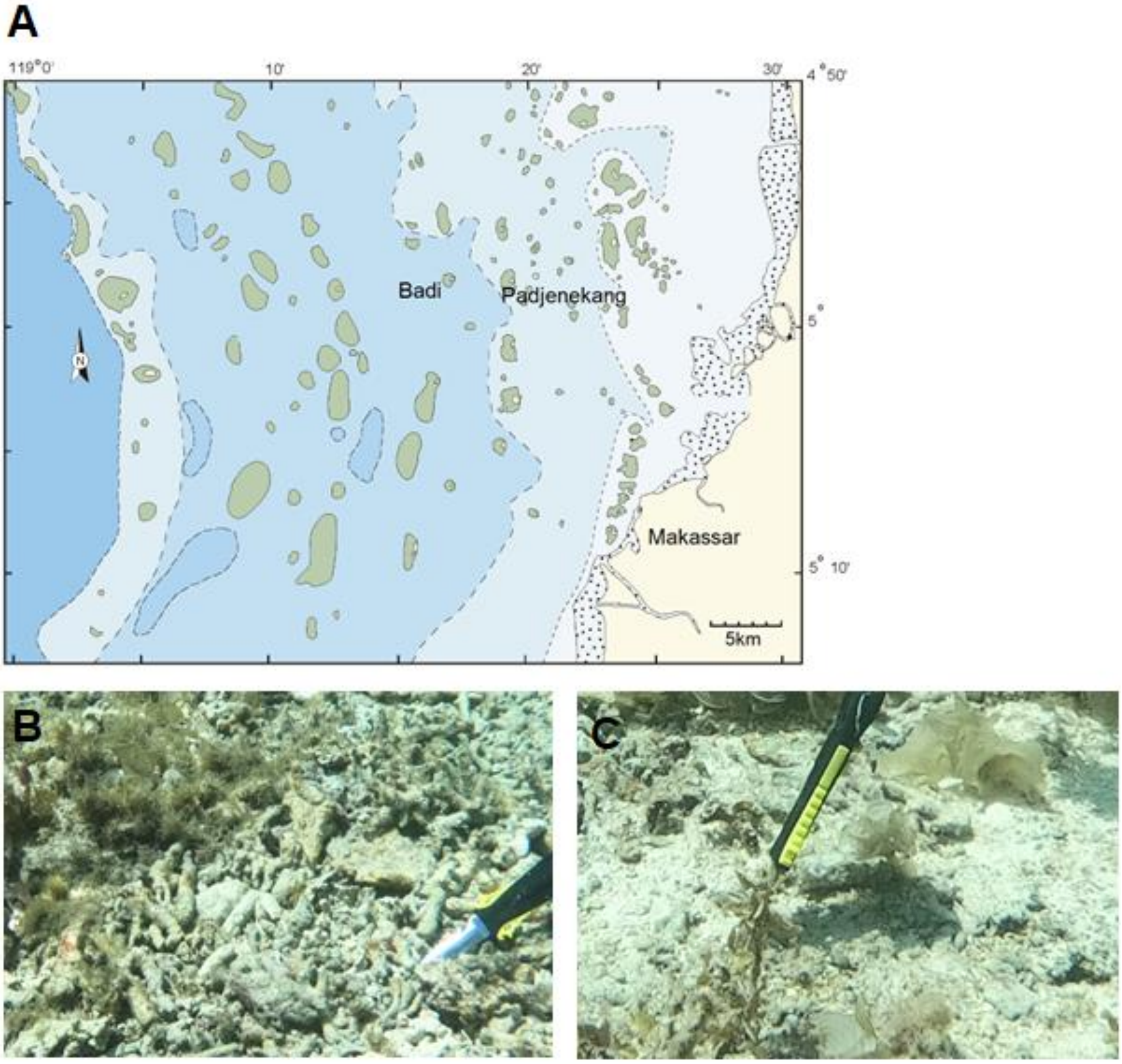

Fig.1A. Spermonde Archipelago, in the Makassar Strait (Indonesia), where the two sampled islands Badi and Padjenekang are located. **B.** In Badi, the substrate is a mix of macroalgae and coral rubble covered by crustose coralline algae. **C.** In Padjenekang the substrate was mainly composed of sand and coral rubble covered by crustose coralline algae.

Sampling

During August 2022, seawater from the benthic boundary layer (from now on, referred to as seawater), substrate and living assemblages of LBFs were collected from Badi and Padjenekang (Fig.1) at three sites: reef flat, the reef slope at water depths of 10 m and 20m.

Water sampling:

At each sampling site, seawater at 1-10 cm from the substrate was collected three times using 50 mL syringes and stored in a cooling box filled with ice. The collected seawater was then filtered through sterile 0.2µm pore-size filters (Whatman Puradisc 25mm), and the filters were placed in ATL lysis buffer (Blood and Tissue DNA extraction kit, Qiagen) at room temperature for transportation to the Naturalis Biodiversity Centre (NBC) for DNA extraction.

Substrate sampling

For the substrate samples, a 50mL falcon tube was filled with the collected substrate (rubble, sand, or algae) at each sampling site. These tubes were then stored in 70% ethanol inside a cooling box filled with ice. Upon returning to shore, the samples were carefully examined under a microscope to remove all visible Larger Benthic Foraminifera (LBFs), as the objective was to study the microbiome of the substrate by itself. Subsequently, samples were transferred to 96% ethanol and stored at -20°C until DNA extraction was conducted at the NBC.

Foraminifera sampling:

Finally, the foraminifera sampling consisted of filling cotton bags (18 cm x 32 cm) with rubble, algae and/or sand from the substratum. Once out of the water, the surface of the substrate, the coral rubble or algae was scrapped to collect all the LBFs specimens inhabiting their surface. Each scrapped material was stored in separated tubes with 96% ethanol at -20 ºC till the foraminifera picking and DNA extraction was performed at the NBC.

From each sample, 5 healthy individuals of the following target species were picked using a stereomicroscope: *Amphistegina radiata, A. lessonii, A. lobifera, Calcarina spengleri,* *Heterostegina depressa* and *Neorotalia calcar.* Colour was used to distinguish between healthy and deceased individuals, as it indicates the presence of photosymbionts. These particular species were chosen because they are all known to be diatom-bearing as well as present smooth tests, which are expected to facilitate the cleaning process (refer to DNA extraction section). Pictures were taken, and the individuals were identified to the species level based on morphological features of their tests, following the criteria outlined in Macher et al. (2021), Renema (2018), Renema et al. (2001), and the World Foraminifera Database. In total, 100 individuals were selected and carefully stored in separate tubes with Ethanol 96% to prevent any potential cross-contamination.

Due to their varying distribution along the reef, not all species were present in every area. On the reef flat, *A. lessonii, A. lobifera*, and *N. calcar* were present. In the mid-reef slope (10m), *A. lessonii, A. radiata, H. depressa,* and *C. spengleri* were found. Lastly, in the deep reef slope (20m), the collected species were *A. lessonii, A. radiata,* and *H. depressa* (Fig.2).

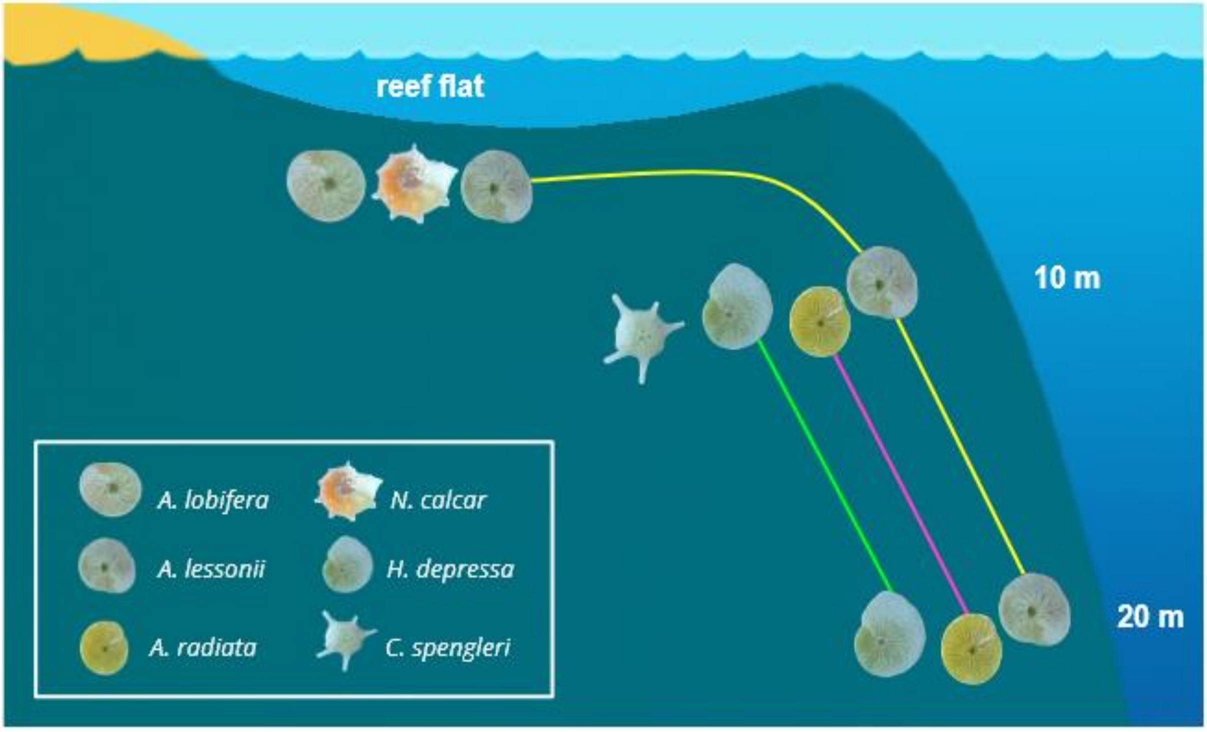

Fig. 2. Distribution of the LBFs along the three different sampled areas of the reef (reef flat, reef slope at 10 and 20 m). *A. lessonii* was present across all the areas (yellow line) and, *A. radiata* and *H. depressa* were present along the reef slope (pink and green lines).

DNA extraction

DNA extractions were carried out in February of 2023 at the Naturalis Biodiversity Centre (NBC). DNA was extracted from a total of 18 seawater samples with the DNeasy 96 Blood & Tissue Kit (Qiagen) with a modified protocol to maximise DNA yield (Annex 1). The DNA from the 6 substrate samples were extracted with the NucleoSpin Soil Kit (Macherey-Nagel) with a modified protocol (Annex 2).

The DNA extraction of 100 foraminifera individuals had a previous cleaning step to thoroughly eliminate external microorganisms and organic matter from the shells. First, they were brushed with a thin brush and transferred to a new individual tube containing clean ethanol 96%. The utensils used in this step were sterilised between cleaning of each individual. Then, the specimen was rinsed three times with MiliQ water, with vortexing carried out between each rinse to enhance the removal of remaining impurities. Finally, the cleaned individuals were stored in a new tube filled with Ethanol 96%. Before DNA extraction, each individual was dried in 1.5-ml Eppendorf tubes and then crushed using a sterile metal pestle. The QIAamp DNA Micro Kit (Qiagen) was utilised for total genomic DNA extraction, following the manufacturer's protocol.

To serve as negative controls, for seawater, substrate and foraminifera extractions the same method was carried out in tubes without any biological samples. Following extraction, DNA quantification was conducted using the UV/Vis absorbance spectrometer Lunatic, following the manufacturer's instructions.

Because different kits have an impact on the species abundance, but not on the presence of exact sequence variants (ESVs) (Hallmaier-Wacker et al., 2018), the comparison between seawater, substrate and foraminifera could only be done with presence/absence data (see data analysis section).

Amplification, sequencing and amplicon curation

The target variable regions V4-V5 of the 16S rRNA gene were amplified in all the samples using the primers 515F-Y (5’GTGYCAGCMGCCGCGGTAA) and 926R (5’ CCGYCAATTYMTTTRAGTTT) (Parada et al., 2016). These amplifications were performed by a two-step polymerase chain reaction (PCR) to first amplify the target region 16S and second, to label the DNA using IDT 10-bp unique dual indexes (UDI).

The mastermix for the first PCR consisted of 12.5µL of KAPA HiFi HotStart ReadyMix (Roche, Basel, Switzerland) plus 1µL of each primer (10 pmol/µL of IDT10-515F-Y and IDT10-926-R), 3µL MiliQ and 2.5µL of sample. The PCR programme was 3 min at 95ºC (initiate denaturation), 20 sec at 98ºC (denaturation), 30 sec at 50ºC (annealing), 30 sec at 72ºC (extension) for 35 cycles and 5 min at 72ºC (final extension). For each sample, three PCR replicates were created. PCR products were then purified using magnetic beads. The bead ratio was 0.9µL for each 1µL of sample, and the elution volume was 20µL.

The second PCR aimed to label the samples with the IDT10 labelling kit. The mastermix consisted of 10uL of KAPA HiFi HotStart ReadyMix (Roche, Basel, Switzerland), 1µL of each tagged primer (IDT10-i5 and IDT10-i7), 3µL MiliQ and 3µL of sample. The PCR program was the same as the first PCR but with 8 cycles.

During the amplification stage, various dilution methods were tested (x1, x10, and x50) for the DNA templates. The effectiveness of each dilution method varied depending on the sample. Therefore, the most appropriate dilution method (from 1X to 50X) for each specific sample was selected to ensure optimal results during the amplification process. The purified PCR products were quantified using a Fragment Analyzer. To ensure even representation during sequencing, the IDT10 labelled amplicons were pooled in equimolar ratios. Finally, the pooled samples were sequenced as 250 paired-end reads on an Illumina Novaseq platform.

The sequence data was processed in APSCALE using VSEARCH (Buchner et al., 2022) to correct amplicon errors, identify chimaeras, and merge paired-end reads. The minimum overlap was set to 50 bp with a maximum difference of 10 bases. The length filtering was 367-377 bp, the minimum dereplication was 4, and the clustering alpha was 2 with a minimum abundance of 20 sequences. After processing, the dataset was curated using LULU (Frøslev et al., 2017) default settings. Subsequently, taxonomic assignment for each Exact Sequence Variant (ESV) was assigned using the reference database SILVA 16S rRNA (Pruesse et al., 2007). Taxa were assigned to a certain taxonomic level according to cut-off points of the percentage of identity (ID), which are: 98.7% for species, 94.5% for genus, 86.5% for family, 82% for order, 78.5 for class and 75% for phylum (Yarza et al., 2014).

Software for data analysis

All data filtering and processing were conducted using RSoftware v4.3 (R Core Team 2023), primarily utilising the following packages: *phyloseq* v1.44 (McMurdie & Holmes, 2013) and *microbiome* v1.23 (Lahti & Shetty, 2017). For statistical analysis and visualisation, additional specific packages were employed, and the most important functions will be mentioned in the subsequent sections where they were used.

Contaminants

The *decontam* v1.20 package (Davis et al., 2018) was utilised to detect contaminants by analysing the negative controls. However, in this case, it led to identifying potential non-contaminants as contaminants like cyanobacteria and vice versa, such as *Cutibacterium acnes*. Consequently, the first 50 most abundant ESVs with over 98.7% identification (Yarza et al., 2014) were checked manually to identify major potential contaminants. As a result, a total of 8 ESVs were removed from the dataset *(Burkholderia pseudomultivorans, Cutibacterium acnes, Moraxella osloensis, Klebsiella aerogenes KCTC 2190, Escherichia fergusonii ATCC 35469, Streptococcus oralis subsp. Dentisani and Streptococcus oralis subsp. tigurinus AZ_3a)* if present in every negative sample. These ESVs are extensively documented in the literature as being exclusively associated with the human microbiome.

Data filtering and replicate merging

ESVs assigned to organelles were removed from the data set. Then, those ESVs with read counts below 100 (representing 0.1% of the total minimum reads) in any given sample were excluded from the analysis as they were considered non-present in that sample. Prevalence and rarefaction filtering were avoided to retain rare taxa that could potentially account for disparities among samples (Willis, 2019). Then, the ESVs present in at least 2 out of 3 PCR replicates of a sample were combined. Also, after this filtering, two samples were removed as they did not have any ESV: one sample of *A. lessonnii* and *H. depressa* from Badi island at 20m.

Data analysis

Rarefaction curves were built with *rarecurve()* from the *vegan v2.6* package (Oksanen et al., 2023). To capture all the sequencing depth, ESVs with low abundance reads should also be taken into account. For this, the replicates were merged without removing low-abundant ESVs.

In the alpha diversity analysis, three metrics were calculated and visualised using the *boxplot_alpha()* function in the *microbiome* package. Richness was determined as the total number of ESVs in each sample, complemented by the use of Shannon's diversity index (H') to consider species abundances. A higher H' value indicates a greater number of species and evenness in their abundance. To test the statistical differences between alpha diversity results, the Wilcox test was done.

The Non-Metric Multidimensional Scaling (nMDS) was conducted using a Jaccard dissimilarity matrix based on the filtered data. The method Jaccard was chosen, as it only takes into account presence/absence data. The DNA extraction of water, substrate and foraminifera was made using different extraction kits, which prevents the comparison of abundances (Hallmaier-Wacker et al., 2018). The resulting nMDS plot was visualised using the *plot_ordination()* function from the *phyloseq* package. To assess the impacts of the factors on the dissimilarity patterns observed in the nMDS plot, the Randomization of Residuals in a Permutation Procedure (RRPP) (Collyer & Adams, 2018) was applied to the dissimilarity matrices. The factors tested were sample types (each of the foraminifera species, substrate, and seawater), reef area (reef flat, slope at 10m, and slope at 20m), and island (Badi and Padjenekang). Subsequently, a pairwise test for each factor was performed against a null model to determine their significance ($\alpha < 0.05$).

The ESVs were grouped to examine the relative abundance of each class. To ensure accurate assignments for all ESVs, class level was selected as not all ESVs met the 86.5% threshold needed for family assignment (Yarza et al., 2014), making class the more suitable choice for straightforward grouping. This agglomeration process gave insights into the distribution of different taxonomic groups within the microbial community. The overall most abundant classes were plotted for each of the foraminifera species using the *plot_composition()* function from the *microbiome* package v1.23 (Lahti & Shetty, 2017).

To visualise the number of shared ESVs among foraminifera, substrate, and seawater, as well as between the islands and reef areas, Venn diagrams were created. This was achieved using the *get_vennlist()* function from the *MicrobiotaProcess* v1.12 package (Xu et al., 2023) and the *ggVennDiagram()* function from the *ggVennDiagram* v.1.2 package (Gao et al., 2021). For displaying the shared ESVs between the foraminifera species, an upset diagram was generated. This process involved using the *get_upset()* function from the *MicrobiotaProcess* package, along with the *make_comb_mat()* and *UpSet()* functions from the *ComplexHeatmap v2.16* package (Gu et al., 2016). These visualisations allowed for a clear representation of the overlapping ESVs between the different factors.

In this study, the core microbiome was defined as the set of ESVs that were present across 90% of the subset samples. In this case, the subsets were each foraminifera species, the seawater and the substrate. It is important to note that the definition of the core microbiome does not yet have a consensus within the scientific community (Neu et al., 2021). However, for this specific analysis, a prevalence threshold of 90% was considered appropriate to allow for a single drop-off for every 10 samples, accounting for the variability that may arise in a natural community. The core microbiome was identified with the function *core_members()* in the *microbiome* package v1.23 (Lahti & Shetty, 2017).

RESULTS

The rarefaction curve analysis demonstrated that the sequencing depth was sufficient at around 5x10^5 to capture all the diversity present in most of the foraminifera and substrate samples (Fig. 3A and B). After data filtering, a total of 1345 prokaryotic ESVs were obtained (Annex 3). Among these ESVs, 578 (43%) were found in the foraminifera samples, 625 (45%) in the seawater samples, and 234 (17%) in the substrate samples. The total number of reads was 6,628,125. The lowest number of reads for one ESV was 100 and the maximum was 477,667. The minimum number of reads in one sample was 228 and the maximum was 249,467 (Fig. 3C).

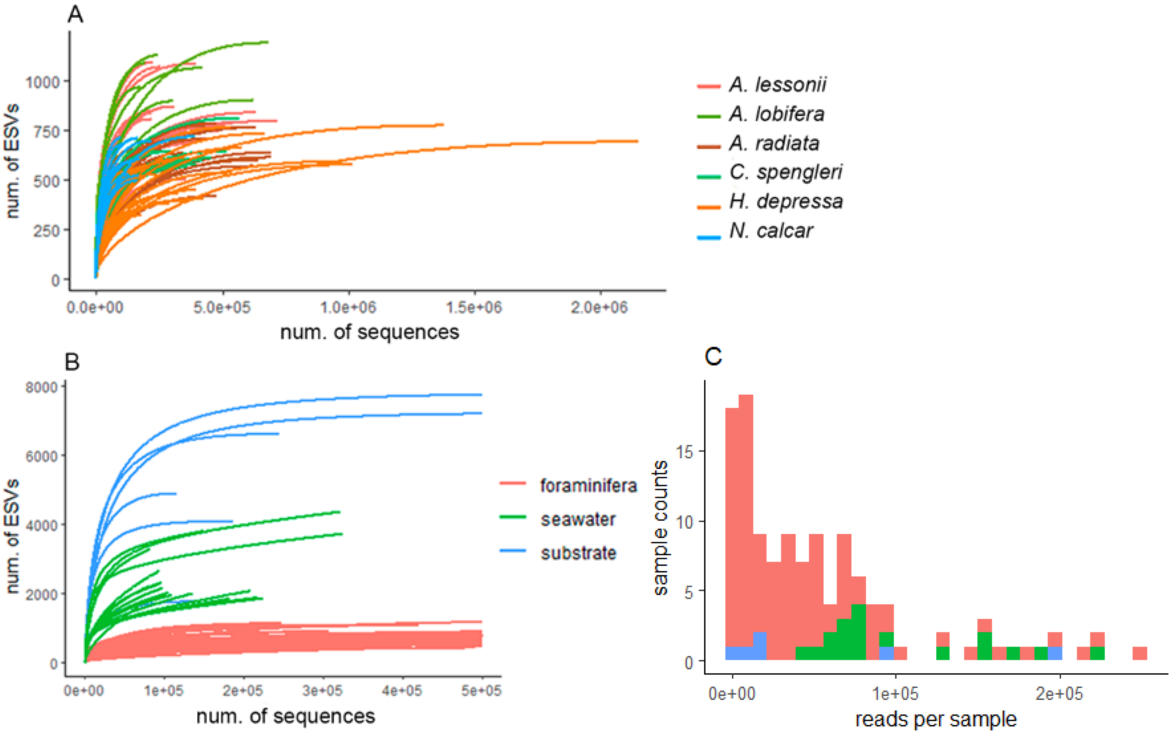

Fig.3. **A.** Rarefaction curve of each foraminifera sample, coloured by species, based on amplicon sequencing of the V4-V5 region of the 16S rRNA gene. The sequencing depth was sufficient to capture most of the diversity in every sample. **B.** Rarefaction curve for each sample. The sequencing depth was sufficient at around 5x10^5 to capture all the diversity present in most of the foraminifera and substrate samples. **C.** Distribution of the total number of reads. This plot shows how most of the samples had less than 1x10^5. Foraminifera samples (in red) were the ones that reached a higher number of reads. Substrate samples (in blue) had the lowest number of reads.

Alpha diversity

The seawater samples had the highest richness and H' diversity, as well as variability, being significantly different from the foraminifera (Wilcox test p-value=1.2e^{-10} for richness and 0.3e^{-9} for H' diversity) and substrate (p-value=0.0300 and 0.0400). Among foraminifera species, all the foraminifera species had similar richness and H' diversity, except for *H. depressa,* which showed the lowest values. This species was the only one that was significantly different from the rest, specifically from *A. lessonii* (p-value=0.0003 and 0.0002), *C. spengleri* (p-value=0.0090 and 0.0149) and *N. calcar* (p-value=5.4 e^{-6} and 0.0041) (Fig. 4).

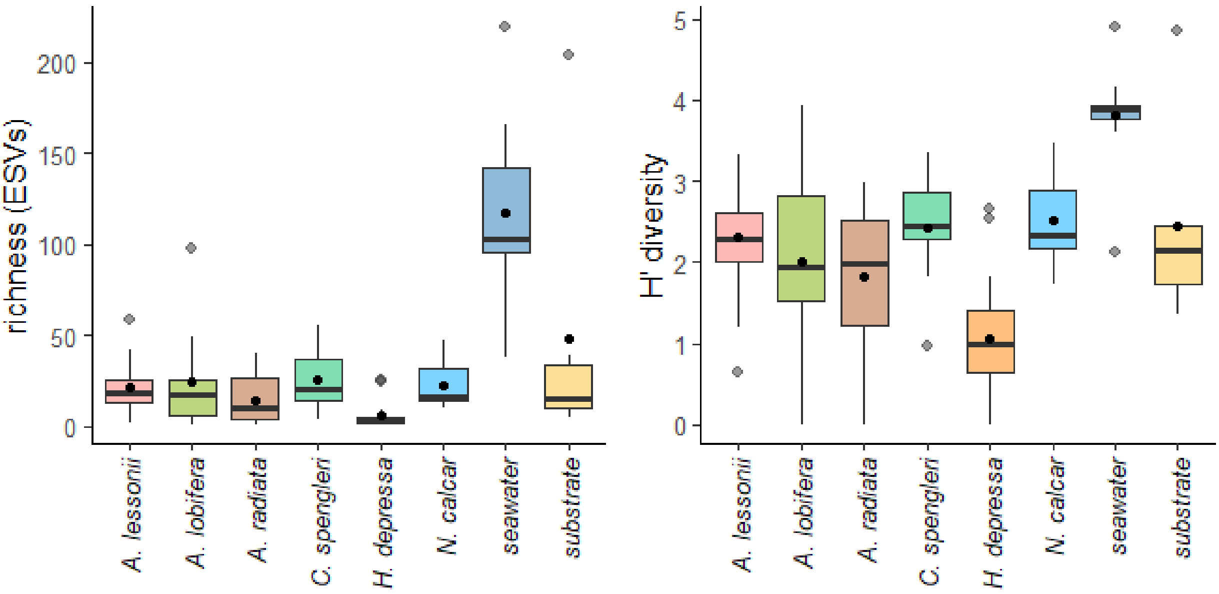

Fig.4. Richness and Shannon's diversity index (H') of the foraminifera *Amphistegina lessonii, A. lobifera, A. radiata, Calcarina spengleri, Heterostegina depressa, Neurotalia calcar,* as well as seawater and substrate samples, based on amplicon sequencing of the V4-V5 region of the 16S rRNA gene Black dots represent the mean and grey dots represent outliers. In order to improve visualisation, a richness value of 665 was not represented in the seawater boxplot.

Beta diversity

Sample type was the main driver of prokaryotic community composition, with an R square up to 22% in the RRPP analysis ((Fig. 5 and Table 1). However, the island and the reef area also had an influence on the composition. The prokaryotic community of the LBFs species was very different from the surrounding environment water and the substrate (p-value <0.05, Annex 4A), although seawater samples showed the most distinct community composition (RRPP pairwise, p-value=0.01). Overall, each LBFs species had a distinct prokaryotic composition, except for some few similarities between some pairs of species. Both reef flat species *A. lobifera* and *N. calcar* did not show differences with *A. lessonii,* and both the reef slope species *A. radiata and C. spengleri* (see Annex 4A for all p-values).

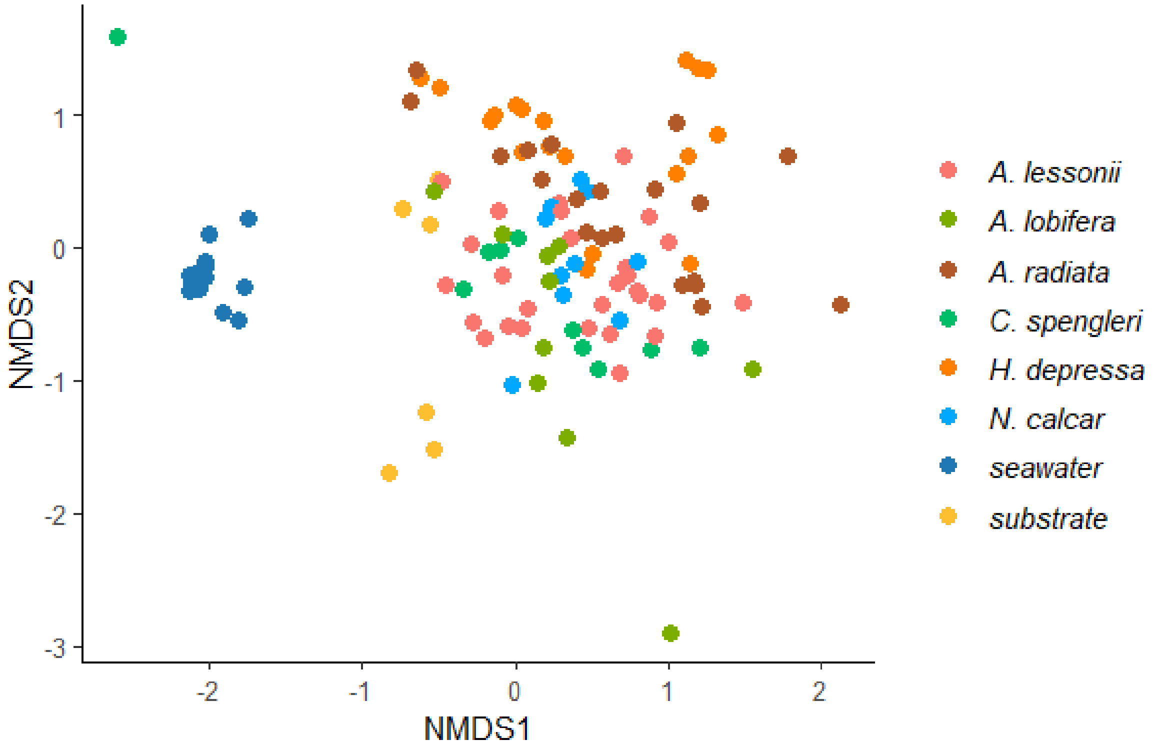

Fig. 5. nMDS of the prokaryotic community based on amplicon sequencing of the V4-V5 region of the 16S rRNA gene in the foraminiferas *Amphistegina lessonii, A. lobifera, A. radiata, Calcarina spengleri, Heterostegina depressa, Neurotalia calcar,* as well as seawater and substrate. Conducted on the Jaccard dissimilarity matrix.

Table 1. Randomization of Residuals in a Permutation Procedure (RRPP) for the prokaryotic communities between sample type (seawater, substrate and each of the 6 species of LBFs), island (Badi and Padjenekang) and area of the reef (reef flat, reef slope at 10 and 20 m depth), and all their interactions. Based on amplicon sequencing of the V4-V5 region of the 16S rRNA gene and conducted on the Jaccard dissimilarity matrix (α=0.05).

Factor	R^2 (%)	p-value
Sample type	22.17	0.001*
Island	2.53	0.001*
Area	2.40	0.001*
Sample type:island	6.41	0.001*
Sample type:area	4.79	0.001*
island:area	1.69	0.001*
Sample type:island:area	3.89	0.005*

The prokaryotic communities in both islands are strongly influenced by sample type (Rs=31%, p-value=0.001), but also by the area of the reef (Rs=4-5%, p-value=0.001, Annex 4B). The LBFs-associated community consistently differed from the seawater and substrate (Annex 4C). Exploring the inter-island disparities, LBFs from Padjenekang exhibited a higher degree of similarity among them, than those from Badi. Within Badi, the prokaryotic communities found within LBFs samples exhibited a greater dispersion (Fig. 6), suggesting a more species-specific association. However, despite these differences, in both islands, certain LBFs exhibited significant similarities in their prokaryotic communities (Annex 4C).

When examining the prokaryotic community of the LBFs along the reef areas within each island, Badi only displayed differences between the two areas of the reef slope. In contrast, Padjenekang exhibited notable disparities, particularly between the 10-meter slope and the rest of the areas (see Annex 4D for all p-values). Those species that occurred across the reef also showed significant differences in their microbial composition depending on the area (Annex 4E).

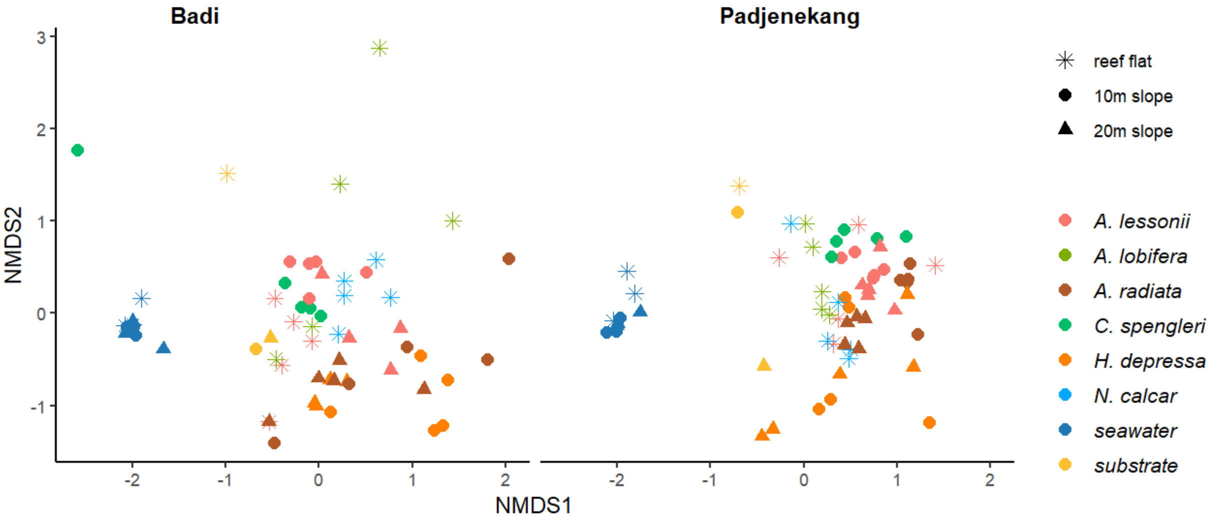

Fig. 6. nMDS of the prokaryotic community in the Larger Benthic Foraminifera species *Amphistegina lessonii, A. lobifera, A. radiata, Calcarina spengleri, Heterostegina depressa, Neurotalia calcar,* as well as seawater and substrate, for each island and reef area. Based on amplicon sequencing of the V4-V5 region of the 16S rRNA gene and conducted on the Jaccard dissimilarity matrix.

Classes abundance in the LBFs

The abundance of the prokaryotic classes sequenced in this study varied across samples, as well as between islands. Overall, the most abundant classes were Gammaproteobacteria, Alphaproteobacteria and Bacilli, although their abundances changed between species (Fig. 7A). For most of the species Gammaproteobacteria was the most abundant class, except for *A. lessonii* and *A. lobifera.* For both of these species the most abundant class was Alphaproteobacteria and they were also the only ones where Myxococcia was found, supporting the similarities found throughout all the results. *N. calcar* had the most unique abundance distribution, with a high abundance of Clostridia and the unique presence of Vicinamibacteria.

When distinguishing between islands, both show similar abundance and presence patterns for each species (Fig. 7B). However, in Badi there is a major presence of the class Bacteroidia when present, while in Padjenekang the class Bacilli has a higher abundance and Alphaproteobacteria is lower. *N. calcar* is the species that have a more different class abundance between islands, as Clostridia and Vicinamibacteira is only part of its microbiome in Padjenekang by a reduction of the proportion of Alphaproteobacteria.

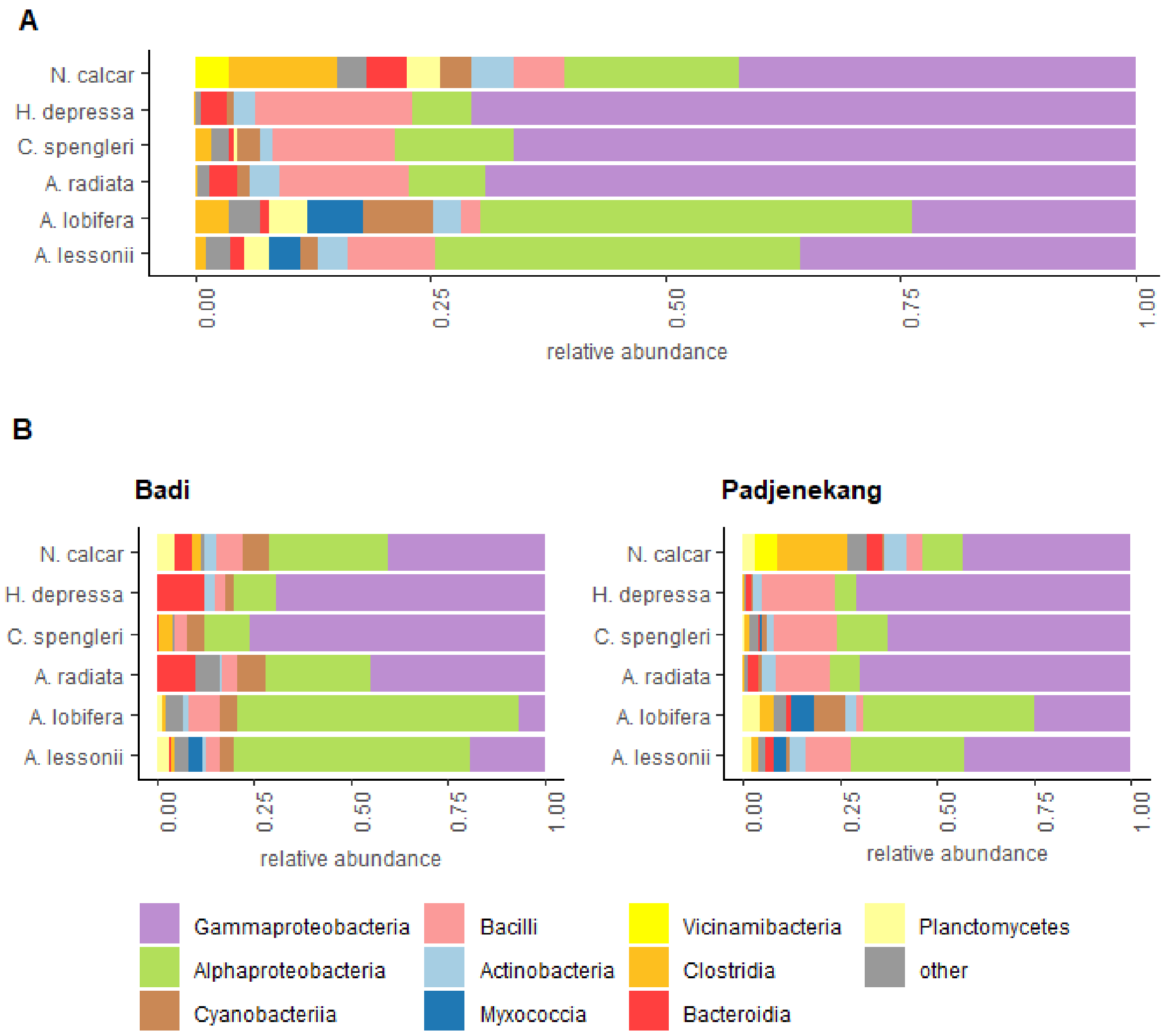

Fig. 7. Relative abundance of the prokaryotic classes based on amplicon sequencing of the V4-V5 region of the 16S rRNA gene found in the six species of the Larger Benthic foraminifera sampled in the Spermonde Archipelago **(A)**, as well as in each sampled island **(B)**.

Shared ESVs

n examining the shared ESVs between the foraminifera and the environment, there is a high level of specificity in the microbial compositions between the foraminifera, the seawater and the substrate, as already pointed out by the nMDS and the RRPP analysis. Out of the 1345 sequenced prokaryotic ESVs, a significant portion is exclusively present with foraminifera (37%), substrate (13%), and in seawater (44%; Fig 8A). The proportions of ESV shared between the foraminifera and the seawater or substrate is very low, as well as between the seawater and substrate (maximum of 3%). Regarding the LBFs prokaryotic community, islands Badi and Padjenekang shared 18% of the ESVs, and Padjenekang had triple the amount of exclusive ESVs than Badi (Fig. 8B). The reef areas shared a low proportion of ESVs in both islands, between 6 and 8%. The highest proportion of unique ESVs in Badi was found in the slope at 10 m depth (44%) and the reef flat in Padjenekang (41%) (Fig. 8C).

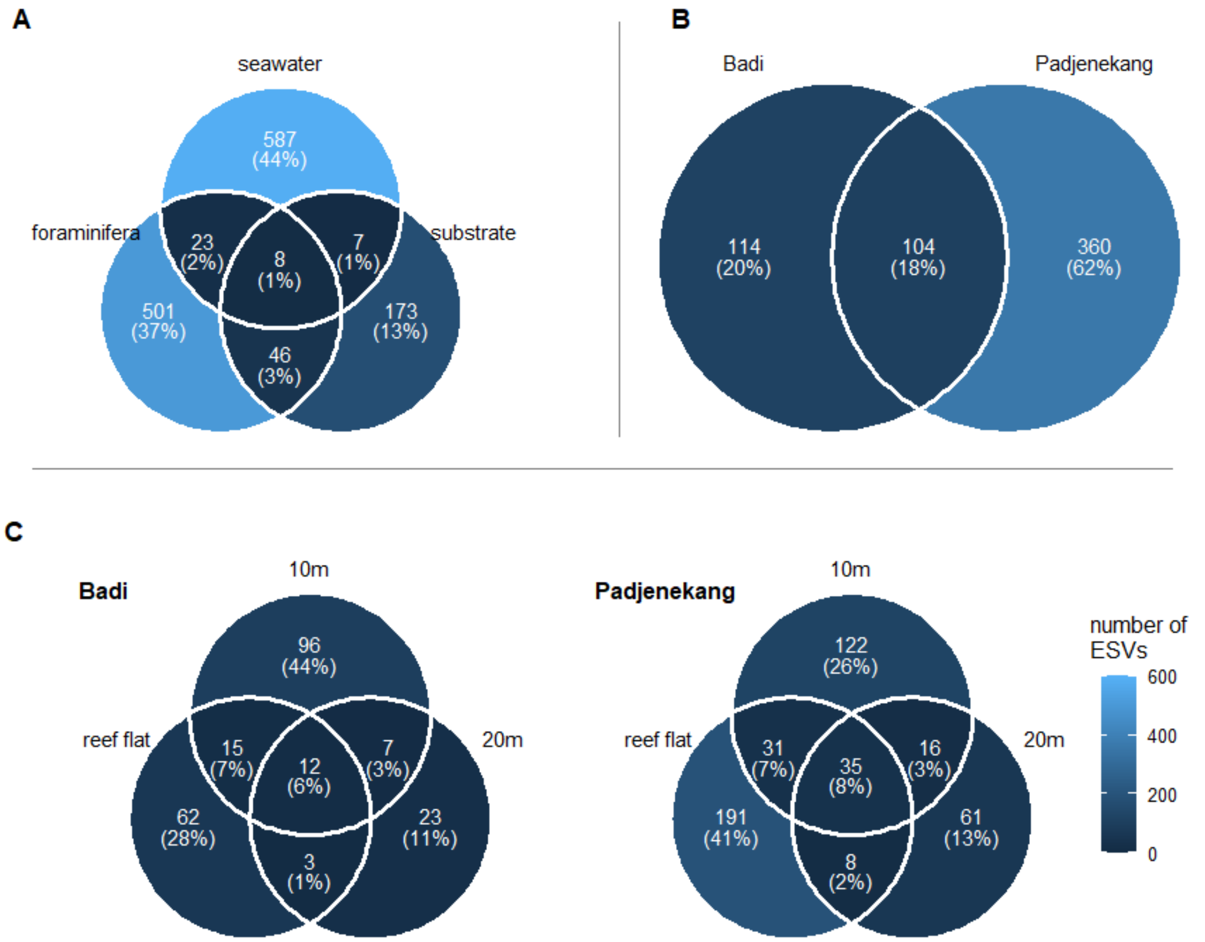

Fig. 8. Venn diagram of all the shared and exclusive ESVs based on amplicon sequencing of the V4-V5 region of the 16S rRNA gene. The total number of ESVs are represented in a gradient from dark blue to light blue. **A.** Venn diagram of shared ESVs between the Larger Benthic Foraminifera (LBFs), substrate and seawater samples. **B.** Venn diagram of shared ESVs between the LBFs sampled in each island, Badi and Padjenekang. **C.** Venn diagram of shared ESVs between the LBFs sampled in each area of the reef (reef flat, reef slope at 10 and 20 m depth) in each island.

Upon analysing those 501 exclusive ESVs for the LBFs represented in Fig. 8A, the results demonstrate unique microbial characteristics associated with each species, with limited overlap in the ESVs shared between them (Fig.9): 25% are unique to *A. lessonii,* 14% to *A. lobifera,* 8% to *A. radiata,* 2% to *H. depressa,* 13% to *N. calcar,* and 15% to *C. spengleri.* The number of shared ESVs between all six species is only 11, highlighting the rarity of common ESVs among them. Furthermore, the majority of possible intersections between species average 2.5 shared ESVs. The only exception to this trend is between *A. lessonii* and *A. lobifera*, which share the higher number of ESVs, totalling 17 and, *A. lessonii* and *A. radiata*, sharing 11 ESVs.

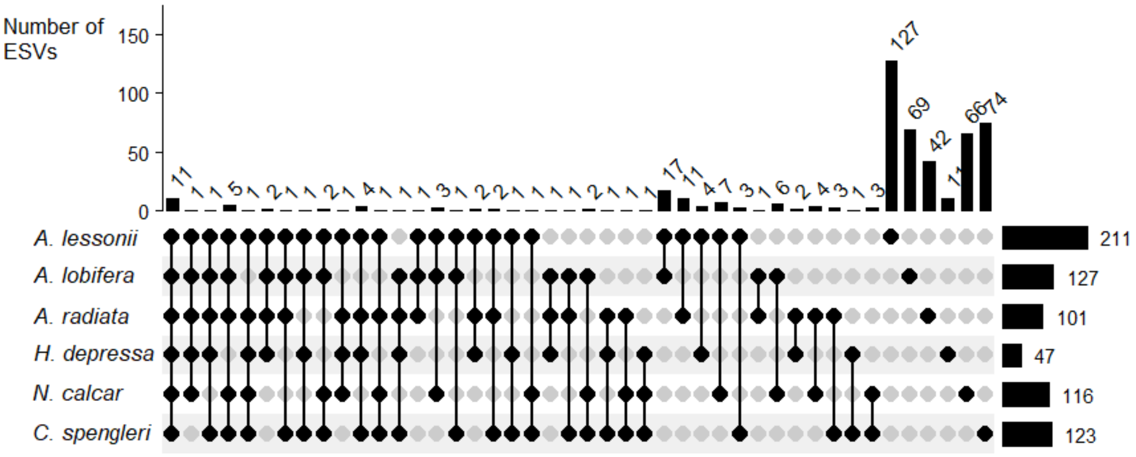

Fig. 9. Upset diagram representing the exclusively shared ESV among the Larger Benthic Foraminifera (LBFs) species based on amplicon sequencing of the V4-V5 region of the 16S rRNA gene. The bar graph indicates the number of ESVs shared by the species marked with a dot in the area below. On the right, the horizontal bars show the total number of ESV present in one LBFs.

Across all LBFs species, the five most abundant prokaryotic ESVs were identified and plotted for all the species (Fig. 10). All ESVs belonging to Gammaproteobacteria class were found in all samples except for the ESV 59 (unclassified Gammaproteobacteria), which exclusively appeared in *C. spengleri*. Furthermore, ESV 27, a Bacilli, displayed a ubiquitous presence in all the reef slope species. ESV 21 appeared not only in all reef slope species but also in *C. spengleri.*

Interestingly, certain LBFs species exhibited distinctive prokaryotic ESV dominance. For instance, *H. depressa* showcased a significant prevalence of ESV 18 (Gammaproteobacteria, Pseudomonadales,) while *N. calcar* exhibited a high dominance of ESV 11 (Gammaproteobacteria, Burkholderiales). *C. spengleri* and *A. radiata* both displayed a strong affiliation with ESV 15 (Gammaproteobacteria, Xanthomonadales), while *A. lobifera* was predominantly associated with ESV 85 (Alphaproteobacteria, Rhodobacterales). *A. lessonii* stood out with ESV 21 (Alphaproteobacteria, Rhodobacterales) and ESV 15 (Gammaproteobacteria, Burkholderiales) as its dominant ESVs.

Those described associations between LBFs species and the different ESVs are maintained in both island (Fig. 10). However, in Padjenekang there is a strong presence of two *Bacilli* (ESV 27 and ESV37) and two Gammaproteobacteria (ESV25 and ESV35) that are not present in Badi.

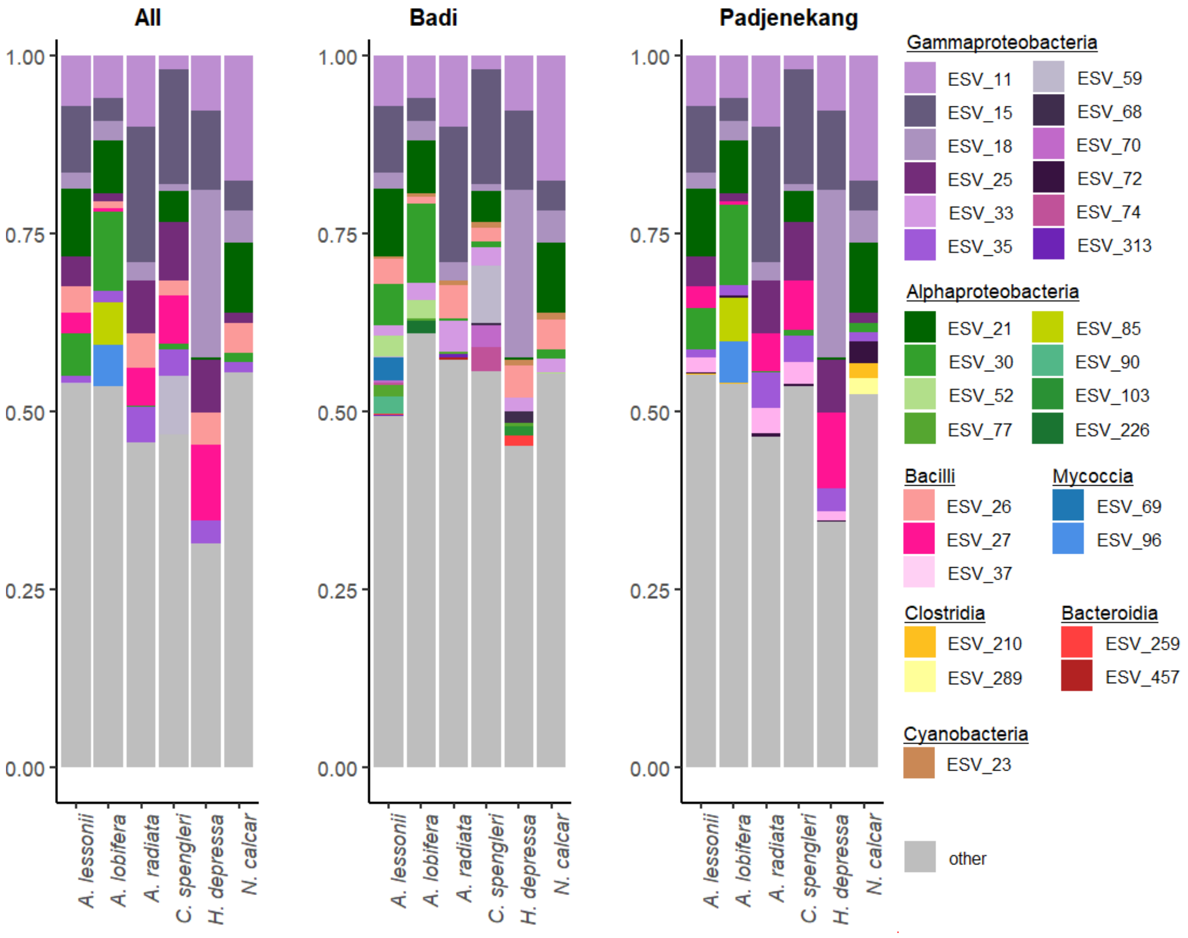

Fig 10. Relative abundance of the most abundant prokaryotic ESVs in each Larger Benthic Foraminifera species, as well as their composition in each sampled island, Badi and Padjenekang. The ESVs are grouped in classes by colour. Based on amplicon sequencing of the V4-V5 region of the 16S rRNA gene.

Core microbiome

Table 2. LBFs species-specific core prokaryotic microbiome composition each in the different areas. The core microbiome ESVs are defined as present in at least 90% of the samples. The first column corresponds to the core microbiome of the overall samples of each species. For each island, Badi and Padjenekang, the core microbiome was identified for each of the reef areas (reef flat and reef slope at 10 m and 20 m depth). Each ESV is coloured based on the taxonomic class: Gammaproteobacteria, Alphaproteobacteria, Cyanobacteria, Bacilli and Actinobacteria. Those areas where the foraminifera species were not present are indicated with a dash (-). The word *none* is used when no ESV was identified as core microbiome.

	Overall	Badi			Padjenekang		
		Reef flat	Slope 10 m	Slope 20 m	Reef flat	Slope 10 m	Slope 20 m
A. lessonii	none	ESV_23	ESV_11 ESV_21 ESV_30 ESV_90 ESV_107	ESV_11	none	ESV_11 ESV_15 ESV_18 ESV_21 ESV_25 ESV_26 ESV_27 ESV_37 ESV_67	ESV_11 ESV_18 ESV_30 ESV_57
A. lobifera	none	none	-	-	ESV_11 ESV_15 ESV_23 ESV_30 ESV_31 ESV_33 ESV_35	-	-
A. radiata	none	-	none	none	-	ESV_11 ESV_15 ESV_33 ESV_18	ESV_11 ESV_23
H. depressa	none	-	ESV_18	ESV_23	-	ESV_18	none
N. calcar	ESV_11	ESV_11 ESV_21 ESV_25 ESV_26	-	-	ESV_11 ESV_23	none	-
C. spengleri	none	-	ESV_59 ESV_70 ESV_74	-	none	ESV_15 ESV_25 ESV_26 ESV_27 ESV_35 ESV_37 ESV_60	none

Results show that there is no LBFs-shared core prokaryotic microbiome nor species-specific across all the sampled areas. It is only when analysing the core microbiome in each area on each island separately that a species-specific core microbiome was detected, reinforcing the site-specific microbiome identified (Table 2). Species found in Padjenekang tend to have a core microbiome, while in Badi a core microbiome is much more unusual. The size of that core varies from 1 up to 9 ESVs per LBFs species. The taxonomic classes involved are Gammaproteobacteria (the most common), Alphaproteobacteria, Cyanobacteria, Bacilli and Actinobacteria, being

Gammaproteobacteria the most common. Specifically, the most common ESVs forming the core microbiome of the LBFs species were three Burkholderiales (Gammaproteobacteria) ESV_11, followed by ESV_15, ESV_18 and a Cyanobacteria ESV_23 (Synechococcales).

On the contrary to the LBFs, the seawater samples showed a big core microbiome with 49 ESVs present in 90% of all the samples included in this study (Annex 5A). The substrate also had a core microbiome across all the samples but it consisted of only 3 ESVs (Annex 5B).

DISCUSSION

In this work, the prokaryotic microbiome of six Larger Benthic Foraminifera (LBFs) and their environment (seawater and substrate) has been studied through the amplification of the variable regions V4-V5 of the 16S rRNA gene. Results show a species-specific and site-dependent prokaryotic microbiome. This microbiome is not shared with the surrounding seawater nor the substrate, suggesting a possible vertical and horizontal transmission of the microbiome.

1. Is the microbiome of the foraminifera the same as the surrounding environment?

The results of this study indicate that the microbiome of foraminifera is very different to those found in the surrounding water and substrate environments (Martin et al., 2019 also found this differenes with seawater). In fact, each of these three compartments demonstrates distinct microbial communities, with minimal sharing of ESVs among them, and no evidence of a shared core microbiome.

Because LBFs live and feed on the substrate, it was expected to find a shared community between them. However, the substrate has its unique composition, with a fairly low richness of ESVs that does not assemble a big core microbiome across the reef. This result is very different from those of Glasl et al. (2019), where the substrate was by far the richest compared to seawater or corals and was similar between sites. However, it is known that reefs have a very complex structure where every substrate can lead to specific microbial communities (Graham & Nash, 2013 and references within; Yong et al., 2018). The results support these observations, as the island and the area of the reef have a strong influence on the overall prokaryotic community of the substrate.

Seawater stands out as the most diverse compartment and was the only one hosting a diverse core microbiome shared across islands and reef areas. Recent studies have exposed a substantial underestimation of its microbial diversity (Galand et al., 2023) and have demonstrated that microbial communities can be similar across a reef (Glasl et al., 2019). It is known that water flow links reef areas, transferring organic and inorganic matter and living organisms (Goreau et al., 1971; Nelson et al., 2023). This high connectivity and its susceptibility to natural cyclic disturbance (Intermediate Disturbance Hypothesis by Wilkinson, 1999), could be an explanation for its highly diverse but still shared microbiome.

2. Is there a species-specific microbiome?

The prokaryotic microbiome of the LBFs exhibits a pronounced species-specificity, that is strongly influenced by the site and distinctly different from the surrounding environment. This means that in different environments, each of the LBFs species host a unique prokaryotic microbiome. Previous studies have also consistently identified a characteristic microbiome within LBFs species (Bourne et al., 2013; Martin et al., 2019; Webster et al., 2016), therefore it is evident that there is a generalised selectivity in the LBFs prokaryotic microbiome.

For most of the LBFs species, there is a core microbiome in most of the sites, that consists of few ESVs. This preference for certain ESVs across the individuals of the same species, which varies across areas of the reef, when the total ESV richness is generally around 70, indicates that the studied LBFs have a flexible core-microbiome that is site-specific. The existence of a variable bacterial microbiome has been proposed as advantageous in adapting to changing environmental conditions (Hernandez-Agreda et al., 2016; Prazeres, 2018; Ziegler et al., 2017) and could help explain the colonisation success of LBFs across many marine ecosystems and geological history. This presence of a particular ESV strongly suggests that a symbiotic relationship exists, with selective feeding or farming being most unlikely. If foraminifera have a preference for one bacterial species as food, this would be reflected in a greater variety of ESVs, since the same bacterial species has multiple ESVs. Moreover, the fact that there is a low sharing of ESVs with their environment, could be due to a vertical and/or horizontal transmission, not only of their symbiotic algae (e.g. Fay et al., 2009; Takagi et al., 2020) but also of their prokaryotic microbiome. However, a more in-depth genetic and physiologic study is needed to confirm a symbiotic relationship.

Amphistegina lessonii and *A. lobifera* have shown a bigger resemblance in their microbiome across all the analyses in this study. The greater taxonomic proximity between them might account for the similarity in their microbiomes, which suggests a possible association between a species' evolutionary lineage and the composition of its microbiome. Moreover, *A. lobifera and A. radiata* have shown some similarities in their prokaryotic composition, with no significant differences found between them. Symbiosis with eukaryotic algae has been proposed as a driving force in the evolution of diatom-bearing foraminifera (Lee, 2006; Lee et al., 2010). Consequently, it is plausible that prokaryotic symbiosis has also participated in this process, but further research needs to be done.

At class level, Gammaproteobacteria, Alphaproteobacteria and Bacilli were the most abundant classes in the LBFs microbiome. These groups have already been consistently identified in several LBFs species although the abundance and relative importance of each group varies across studies and species (Bourne et al., 2013; Prazeres et al., 2017; Webster et al., 2016), as it does for the species in this study. The role that those classes might play in LBFs is difficult to determine, as the diversity of prokaryotes and their traits are enormously diverse.

The abundance of classes exhibits variability among hosts, once again highlighting host species-specific association. Notably, *N. calcar* displays a particularly distinctive composition characterised by a more even abundance of the prokaryotic classes and a high presence of Clostridia and Vicinamibacteria. This species exclusively appeared in the reef flat, and its lack of a strong dominance of a class could be due to that species confined to shallow areas tend to exhibit more diverse microbiomes compared to those of the deeper regions of the Pacific Ocean (Baker, 2003). As of the author's knowledge, the present work is the first study including the microbiome of *N. calcar*, making it challenging to determine whether this composition is specific to the local environment or not. *A. lessonii* and *A. lobifera* were the only species in which Alphaproteobacteria was the most abundant class and where Myxococcia was found, again supporting the idea of similarities between two very evolutionary close species.

H. depressa was found to host the lowest diversity compared to the other studied species and is predominantly composed of Gammaproteobacteria. This is consistent with the findings in (Webster et al., 2016) where Alpha and Gammaproteobacteria were much more dominant in the microbiome of *H. depressa*. However, Bourne et al., (2013), it had the largest abundance of Cyanobacteria compared to other species. These differences between studies support the idea of site-specific prokaryotic microbiome, although different methods can result in bias during amplification.

It has been extensively demonstrated that the choice of DNA extraction method as well as 16S ribosomal regions to sequence leads to bias in the amplification of certain groups over others (Barb et al., 2016; Clooney et al., 2016; Fouhy et al., 2016; Hallmaier-Wacker et al., 2018; Rintala et al., 2017). The referenced studies above on LBFs microbiome use different extraction methods and target other variable regions of the 16S gene (Bourne et al., 2013; Martin et al., 2019; Prazeres, 2018; Prazeres et al., 2017; Webster et al., 2016), so it is to be expected to find disparities in abundances due to this factor. Finally, the reference database for the taxonomic assignation can also cause differences between studies. For instance, the SILVA database (used in this work, as well as in (Prazeres, 2018; Prazeres et al., 2017; Webster et al., 2013, 2016)) considered Burkholderiales as a Gammaproteobacteria, whereas in other databases like GreenGenes is classified as Betaproteobacteria (used in Bourne et al., 2013; Martin et al., 2019). Due to this, it is urgent to establish consensus in the scientific community to use methods that are as similar as possible.

3. Does the microbiome change with island or reef area?

The composition of the microbiome is significantly influenced by both the island and the reef area. Dissimilarities between islands could be attributed to two factors. First, disparities in their substrate composition. Reef sediment characteristics, such as particle composition or carbon content have an important role shaping in its microbial community (Glasl et al., 2019). Each island featured distinct substrates, with Badi characterized by a higher prevalence of algae and Padjenekang exhibiting a greater abundance of sand.

Secondly, the influence of terrestrial factors. Both islands are inhabited, and the composition of the free bacterial community is strongly influenced by water quality, which tends to deteriorate in areas with human presence. Studies conducted in the Spermonde Archipelago region have consistently shown a close relationship between the bacterial community and water quality (Kegler et al., 2017; Polónia et al., 2015). Specifically, low water quality accompanied by a high influx of organic matter can lead to a greater abundance of Gammaproteobacteria, Bacilli, and Bacteroidia (Kegler et al., 2017).

Both islands are inhabited and the free bacterial community is very much influenced by water quality, which tends to decrease with human presence. Studies in this area (Spermonde Archipelago) have shown that the bacterial community is very related to water quality (Kegler et al., 2017; Polónia et al., 2015), and low water quality with a high input of organic matter can result in a higher abundance of Gammaproteobacteria, Bacilli and Bacteroidia (Kegler et al., 2017).

Gammaproteobacteria and Bacilli, have a strong presence in the foraminifera in Padjenekang, and the seawater samples from this area, the order Bacteroidales, often associated with long-term human sewage contamination (Newton et al., 2011), were notably prevalent. In Badi, Alphaproteobacteria becomes very abundant, which is related to a higher concentration of inorganic nutrients in this area (Kegler et al., 2017). However, confirming these associations would require more extensive research, which is beyond the scope of our current work.

Dissimilarities are evident among reef areas. Although the sharing of ESVs between areas is relatively limited, a higher number of shared ESVs is observed among species occupying the same reef area. This is expected, first because not all LBFs were present across all the reef areas and results show that the prokaryotic microbiome is species-specific. For those species that have been sampled across different areas (*A. lessonii, A. lobifera* and *H. depressa)*, results show that their prokaryotic microbiome varies with depth. This effect has also been shown in other studies that have sampled LBFs across different depths (Prazeres, 2018). The reef ecosystem is very heterogenous, where each habitat (Montaggioni, 2005) has its intrinsic environmental conditions (Baumann et al., 2016; Guadayol et al., 2014) that can ultimately influence the prokaryotic microbiome in LBFs (Prazeres et al., 2017).

Conclusions

In summary, this study underscores the intricate interplay between species and local environmental conditions in shaping prokaryotic communities within Larger Benthic Foraminifera (LBFs). These insights offer valuable perspectives into the dynamics of microbial communities in these vital marine habitats, shedding light on the determinants of their diversity and composition. Our findings reveal that the prokaryotic microbiome of LBFs displays a pronounced species and site specificity, distinctly different from the surrounding environment. At the class level, Gammaproteobacteria and Alpha and Gammaproteobacteria emerge as the predominant classes in the LBFs' microbiome, although, the abundance of specific microbial groups varies among species and islands. Furthermore, most LBFs exhibit a core microbiome that exhibits variability within specific sites, suggesting that LBFs species have flexible prokaryotic microbiome depending on the environment. Interestingly, taxonomically closer LBF species tend to harbour more similar microbiomes, suggesting a potential correlation between phylogenetic proximity and microbial community composition among these fascinating marine organisms.

REFERENCES

Ainsworth, T. D., Krause, L., Bridge, T., Torda, G., Raina, J. B., Zakrzewski, M., Gates, R. D., Padilla-Gamiño, J. L., Spalding, H. L., Smith, C., Woolsey, E. S., Bourne, D. G., Bongaerts, P., Hoegh-Guldberg, O., & Leggat, W. (2015). The coral core microbiome identifies rare bacterial taxa as ubiquitous endosymbionts. *ISME Journal*, *9*(10), 2261–2274. https://doi.org/10.1038/ismej.2015.39

Archibald, J. M. (2015). Endosymbiosis and eukaryotic cell evolution. In *Current Biology* (Vol. 25, Issue 19). https://doi.org/10.1016/j.cub.2015.07.055

Baker, A. C. (2003). Flexibility and Specificity in Coral-Algal Symbiosis: Diversity, Ecology, and Biogeography of Symbiodinium. In *Annual Review of Ecology, Evolution, and Systematics* (Vol. 34, pp. 661–689). Annual Reviews Inc. https://doi.org/10.1146/annurev.ecolsys.34.011802.132417

Barb, J. J., Oler, A. J., Kim, H.-S., Chalmers, N., Wallen, G. R., Cashion, A., Munson, P. J., & Ames, N. J. (2016). Development of an Analysis Pipeline Characterizing Multiple Hypervariable Regions of 16S rRNA Using Mock Samples. *PLOS ONE*, *11*(2), e0148047. https://doi.org/10.1371/journal.pone.0148047

Baumann, J. H., Townsend, J. E., Courtney, T. A., Aichelman, H. E., Davies, S. W., Lima, F. P., & Castillo, K. D. (2016). Temperature Regimes Impact Coral Assemblages along Environmental Gradients on Lagoonal Reefs in Belize. *PLOS ONE*, *11*(9), e0162098. https://doi.org/10.1371/journal.pone.0162098

Blackall, L. L., Wilson, B., & Van Oppen, M. J. H. (2015). Coral-the world's most diverse symbiotic ecosystem. In *Molecular Ecology* (Vol. 24, Issue 21, pp. 5330–5347). https://doi.org/10.1111/mec.13400

Bourne, D. G., Dennis, P. G., Uthicke, S., Soo, R. M., Tyson, G. W., & Webster, N. (2013). Coral reef invertebrate microbiomes correlate with the presence of photosymbionts. *ISME Journal*, *7*(7), 1452–1458. https://doi.org/10.1038/ismej.2012.172

Buchner, D., Macher, T.-H., & Leese, F. (2022). APSCALE: advanced pipeline for simple yet comprehensive analyses of DNA metabarcoding data. *Bioinformatics*, *38*(20), 4817–4819. https://doi.org/10.1093/bioinformatics/btac588

Clooney, A. G., Fouhy, F., Sleator, R. D., O' Driscoll, A., Stanton, C., Cotter, P. D., & Claesson, M. J. (2016). Comparing Apples and Oranges?: Next Generation Sequencing and Its Impact on Microbiome Analysis. *PLOS ONE*, *11*(2), e0148028. https://doi.org/10.1371/journal.pone.0148028

Collyer, M. L., & Adams, D. C. (2018). RRPP: An r package for fitting linear models to high-dimensional data using residual randomization. *Methods in Ecology and Evolution*, *9*(7), 1772–1779. https://doi.org/10.1111/2041-210X.13029

Davis, N. M., Proctor, Di. M., Holmes, S. P., Relman, D. A., & Callahan, B. J. (2018). Simple statistical identification and removal of contaminant sequences in marker-gene and metagenomics data. *Microbiome*, *6*(1), 226. https://doi.org/10.1186/s40168-018-0605-2

Erftemeijer, P. L. A. (1993). *Factors limiting growth and production of tropical seagrasses: nutrient dynamics in Indonesian seagrass beds*. University of Bremen, Nijmegen.

Fankboner, P. (1971). Intracellular digestion of symbiontic zooxanthellae by host amoebocytes in giant clams (Bivalvia: Tridacnidae), with a note on the nutritional role of the hypertrophied siphonal epidermis. *The Biological Bulletin*, *141*(2), 222–234.

https://doi.org/10.2307/1540113

Fay, S. A., Weber, M. X., & Lipps, J. H. (2009). The distribution of Symbiodinium diversity within individual host foraminifera. *Coral Reefs*, *28*(3), 717–726. https://doi.org/10.1007/s00338-009-0511-y

Fouhy, F., Clooney, A. G., Stanton, C., Claesson, M. J., & Cotter, P. D. (2016). 16S rRNA gene sequencing of mock microbial populations-impact of DNA extraction method, primer choice and sequencing platform. *BMC Microbiology*, *16*(1), 123. https://doi.org/10.1186/s12866-016-0738-z

Freeman, C. J., Easson, C. G., Fiore, C. L., & Thacker, R. W. (2021). Sponge–Microbe Interactions on Coral Reefs: Multiple Evolutionary Solutions to a Complex Environment. In *Frontiers in Marine Science* (Vol. 8). https://doi.org/10.3389/fmars.2021.705053

Frøslev, T. G., Kjøller, R., Bruun, H. H., Ejrnæs, R., Brunbjerg, A. K., Pietroni, C., & Hansen, A. J. (2017). Algorithm for post-clustering curation of DNA amplicon data yields reliable biodiversity estimates. *Nature Communications*, *8*(1), 1–11. https://doi.org/10.1038/s41467-017-01312-x

Galand, P. E., Ruscheweyh, H.-J., Salazar, G., Hochart, C., Henry, N., Hume, B. C. C., Oliveira, P. H., Perdereau, A., Labadie, K., Belser, C., Boissin, E., Romac, S., Poulain, J., Bourdin, G., Iwankow, G., Moulin, C., Armstrong, E. J., Paz-García, D. A., Ziegler, M., … Planes, S. (2023). Diversity of the Pacific Ocean coral reef microbiome. *Nature Communications*, *14*(1), 3039. https://doi.org/10.1038/s41467-023-38500-x

Gao, C.-H., Yu, G., & Cai, P. (2021). ggVennDiagram: An Intuitive, Easy-to-Use, and Highly Customizable R Package to Generate Venn Diagram. *Frontiers in Genetics*, *12*, 706907. https://doi.org/10.3389/fgene.2021.706907

Girard, E. B., Estradivari, Ferse, S., Ambo-Rappe, R., Jompa, J., & Renema, W. (2022). Dynamics of large benthic foraminiferal assemblages: A tool to foreshadow reef degradation? *Science of The Total Environment*, *811*, 151396. https://doi.org/10.1016/j.scitotenv.2021.151396

Glasl, B., Bourne, D. G., Frade, P. R., Thomas, T., Schaffelke, B., & Webster, N. S. (2019). Microbial indicators of environmental perturbations in coral reef ecosystems. *Microbiome*, *7*(1), 94. https://doi.org/10.1186/s40168-019-0705-7

Goffredi, S. K., Orphan, V. J., Rouse, G. W., Jahnke, L., Embaye, T., Turk, K., Lee, R., & Vrijenhoek, R. C. (2005). Evolutionary innovation: A bone-eating marine symbiosis. *Environmental Microbiology*, *7*(9), 1369–1378. https://doi.org/10.1111/j.1462-2920.2005.00824.x

Goreau, T., Goreau, N. I., & Yonge, C. M. (1971). Reef Corals: autotrophs or heterotrophs? *The Biological Bulletin*, *141*(2), 247–260. https://doi.org/10.2307/1540115

Graham, N. A. J., & Nash, K. L. (2013). The importance of structural complexity in coral reef ecosystems. *Coral Reefs*, *32*(2), 315–326. https://doi.org/10.1007/s00338-012-0984-y

Gu, Z., Eils, R., & Schlesner, M. (2016). Complex heatmaps reveal patterns and correlations in multidimensional genomic data. *Bioinformatics*, *32*(18), 2847–2849. https://doi.org/10.1093/bioinformatics/btw313

Guadayol, Ò., Silbiger, N. J., Donahue, M. J., & Thomas, F. I. M. (2014). Patterns in Temporal Variability of Temperature, Oxygen and pH along an Environmental Gradient in a Coral Reef. *PLoS ONE*, *9*(1), e85213. https://doi.org/10.1371/journal.pone.0085213

Hallmaier-Wacker, L. K., Lueert, S., Roos, C., & Knauf, S. (2018). The impact of storage buffer, DNA extraction method, and polymerase on microbial analysis. *Scientific Reports*, *8*(1), 1–9. https://doi.org/10.1038/s41598-018-24573-y

Hallock, P. (1985). Why are larger Foraminifera large? *Paleobiology*, *2*, 195–208. https://doi.org/10.1017/S0094837300011507

Hallock, P., Lidz, B. H., Cockey-Burkhard, E. M., & Donnelly, K. B. (2003). Foraminifera as bioindicators in coral reef assessment and monitoring: The foram index. *Environmental Monitoring and Assessment*, *81*(1–3), 221–238. https://doi.org/10.1023/A:1021337310386

Hernandez-Agreda, A., Leggat, W., Bongaerts, P., & Ainsworth, T. D. (2016). The microbial signature provides insight into the mechanistic basis of coral success across reef habitats. *MBio*, *7*(4). https://doi.org/10.1128/mBio.00560-16

Humphreys, A. F., Purkis, S. J., Wan, C., Aldrich, M., Nichols, S., & Garza, J. (2022). A New Foraminiferal Bioindicator for Long-Term Heat Stress on Coral Reefs. *Journal of Earth Science*, *33*(6), 1451–1459. https://doi.org/10.1007/s12583-021-1543-7

Kegler, H. F., Lukman, M., Teichberg, M., Plass-Johnson, J., Hassenrück, C., Wild, C., & Gärdes, A. (2017). Bacterial community composition and potential driving factors in different reef habitats of the spermonde archipelago, Indonesia. *Frontiers in Microbiology*, *8*(APR), 185833. https://doi.org/10.3389/fmicb.2017.00662

Lahti, L., & Shetty, S. (2017). Microbiome r package: Tools for microbiome analysis in r. *Bioconductor*, *Microbiome package version 1.23.1.* https://doi.org/https://github.com/microbiome/microbiome

Langer, M. R. (2008). Assessing the Contribution of Foraminiferan Protists to Global Ocean Carbonate Production. *Journal of Eukaryotic Microbiology*, *55*(3), 163–169. https://doi.org/10.1111/j.1550-7408.2008.00321.x

Lee, J. J. (2006). *Algal symbiosis in larger foraminifera*. *42*, 63–75.

Lee, J. J., Cervasco, M. H., Morales, J., Billik, M., Fine, M., & Levy, O. (2010). Symbiosis drove cellular evolution. *Symbiosis*, *51*(1). https://doi.org/10.1007/s13199-010-0056-4

Macher, J. N., Prazeres, M., Taudien, S., Jompa, J., Sadekov, A., & Renema, W. (2021). Integrating morphology and metagenomics to understand taxonomic variability of Amphisorus (Foraminifera, Miliolida) from Western Australia and Indonesia. *PLoS ONE*, *16*(1 January), e0244616. https://doi.org/10.1371/journal.pone.0244616

Margulis, L. (1971). Symbiosis and evolution. *Scientific American*, *225*(2), 48–61.

Martin, M. M., Kellogg, C. A., & Hallock, P. (2019). Microbial Associations of Four Species of Algal Symbiont-bearing Foraminifers from the Florida Reef Tract, Usa. *Journal of Foraminiferal Research*, *49*(2), 178–190. https://doi.org/10.2113/gsjfr.49.2.178

McMurdie, P. J., & Holmes, S. (2013). Phyloseq: An R Package for Reproducible Interactive Analysis and Graphics of Microbiome Census Data. *PLoS ONE*, *8*(4). https://doi.org/10.1371/journal.pone.0061217

Montaggioni, L. F. (2005). History of Indo-Pacific coral reef systems since the last glaciation: Development patterns and controlling factors. *Earth-Science Reviews*, *71*(1–2), 1–75. https://doi.org/10.1016/j.earscirev.2005.01.002

Nelson, C. E., Wegley Kelly, L., & Haas, A. F. (2023). Microbial Interactions with Dissolved Organic Matter Are Central to Coral Reef Ecosystem Function and Resilience. In *Annual Review of Marine Science* (Vol. 15, pp. 431–460). Annual Reviews Inc. https://doi.org/10.1146/annurev-marine-042121-080917

Neu, A. T., Allen, E. E., & Roy, K. (2021). Defining and quantifying the core microbiome:

Challenges and prospects. *Proceedings of the National Academy of Sciences of the United States of America*, *118*(51). https://doi.org/10.1073/pnas.2104429118

Newton, R. J., VandeWalle, J. L., Borchardt, M. A., Gorelick, M. H., & McLellan, S. L. (2011). Lachnospiraceae and bacteroidales alternative fecal indicators reveal chronic human sewage contamination in an Urban harbor. *Applied and Environmental Microbiology*, *77*(19), 6972–6981. https://doi.org/10.1128/AEM.05480-11

Oksanen, J., Simpson, G., Blanchet, F., Kindt, R., Legendre, P., Minchin, P., O'Hara, R., Solymos, P., Stevens, M., Szoecs, E., Wagner, H., Barbour, M., Bedward, M., Bolker, B., Borcard, D., Carvalho, G., Chirico, M., De Caceres, M., Durand, S., … Weedon, J. (2023). *vegan: Community Ecology Package. R package version 2.6-5*. https://doi.org/https://github.com/vegandevs/vegan.

Parada, A. E., Needham, D. M., & Fuhrman, J. A. (2016). Every base matters: Assessing small subunit rRNA primers for marine microbiomes with mock communities, time series and global field samples. *Environmental Microbiology*, *18*(5), 1403–1414. https://doi.org/10.1111/1462-2920.13023

Pernice, M., Raina, J. B., Rädecker, N., Cárdenas, A., Pogoreutz, C., & Voolstra, C. R. (2020). Down to the bone: the role of overlooked endolithic microbiomes in reef coral health. In *ISME Journal* (Vol. 14, Issue 2, pp. 325–334). Springer Nature. https://doi.org/10.1038/s41396-019-0548-z

Polónia, A. R. M., Cleary, D. F. R., de Voogd, N. J., Renema, W., Hoeksema, B. W., Martins, A., & Gomes, N. C. M. (2015). Habitat and water quality variables as predictors of community composition in an Indonesian coral reef: A multi-taxon study in the Spermonde Archipelago. *Science of the Total Environment*, *537*, 139–151. https://doi.org/10.1016/j.scitotenv.2015.07.102

Prazeres, M. (2018). Bleaching-Associated Changes in the Microbiome of Large Benthic Foraminifera of the Great Barrier Reef, Australia. *Frontiers in Microbiology*, *9*(OCT), 2404. https://doi.org/10.3389/fmicb.2018.02404

Prazeres, M., Ainsworth, T., Roberts, T. E., Pandolfi, J. M., & Leggat, W. (2017). Symbiosis and microbiome flexibility in calcifying benthic foraminifera of the great Barrier Reef. *Microbiome*, *5*(1), 38. https://doi.org/10.1186/S40168-017-0257-7

Pruesse, E., Quast, C., Knittel, K., Fuchs, B. M., Ludwig, W., Peplies, J., & Glöckner, F. O. (2007). SILVA: A comprehensive online resource for quality checked and aligned ribosomal RNA sequence data compatible with ARB. *Nucleic Acids Research*, *35*(21), 7188–7196. https://doi.org/10.1093/nar/gkm864

Renema, W. (2018). Terrestrial influence as a key driver of spatial variability in large benthic foraminiferal assemblage composition in the Central Indo-Pacific. *Earth-Science Reviews*, *177*(January), 514–544. https://doi.org/10.1016/j.earscirev.2017.12.013

Renema, W., Hoeksema, B. W., Van Hinte, J. E., Renema, W., Hoeksema, B. W., & Van Hinte, J. E. (2001). Larger benthic foraminifera and their distribution patterns on the Spermonde shelf, South Sulawesi. *Zool. Verh. Leiden*, *334*(29), 115–149. https://repository.naturalis.nl/pub/219452/

Renema, W., & Troelstra, S. R. (2001). Larger foraminifera distribution on a mesotrophic carbonate shelf in SW Sulawesi (Indonesia). *Palaeogeography, Palaeoclimatology, Palaeoecology*, *175*(1–4), 125–146. https://doi.org/10.1016/S0031-0182(01)00389-3

Reveillaud, J., Maignien, L., Eren, M. A., Huber, J. A., Apprill, A., Sogin, M. L., & Vanreusel, A.

(2014). Host-specificity among abundant and rare taxa in the sponge microbiome. *ISME Journal*, *8*(6), 1198–1209. https://doi.org/10.1038/ismej.2013.227

Rintala, A., Pietilä, S., Munukka, E., Eerola, E., Pursiheimo, J. P., Laiho, A., Pekkala, S., & Huovinen, P. (2017). Gut microbiota analysis results are highly dependent on the 16s rRNA gene target region, whereas the impact of DNA extraction is minor. *Journal of Biomolecular Techniques*, *28*(1), 19–30. https://doi.org/10.7171/jbt.17-2801-003

Rosenberg, E., Koren, O., Reshef, L., Efrony, R., & Zilber-Rosenberg, I. (2007). The role of microorganisms in coral health, disease and evolution. In *Nature Reviews Microbiology* (Vol. 5, Issue 5, pp. 355–362). Nature Publishing Group. https://doi.org/10.1038/nrmicro1635

Roth, M. S. (2014). The engine of the reef: Photobiology of the coral-algal symbiosis. In *Frontiers in Microbiology* (Vol. 5, Issue AUG, p. 97199). Frontiers Media S.A. https://doi.org/10.3389/fmicb.2014.00422

Sapp, J. (1994). *Evolution by association: A history of symbiosis*. Oxford University Press. https://doi.org/10.1016/s1369-8486(98)00010-7

Schmidt, C., Heinz, P., Kucera, M., & Uthicke, S. (2011). Temperature-induced stress leads to bleaching in larger benthic foraminifera hosting endosymbiotic diatoms. *Limnology and Oceanography*, *56*(5), 1587–1602. https://doi.org/10.4319/lo.2011.56.5.1587

Takagi, H., Kurasawa, A., & Kimoto, K. (2020). Observation of asexual reproduction with symbiont transmission in planktonic foraminifera. *Journal of Plankton Research*, *42*(4), 403–410. https://doi.org/10.1093/plankt/fbaa033

Titlyanov, E. A., Titlyanova, T. V, Leletkin, V. A., Tsukahara, J., van Woesik, R., & Yamazato, K. (1996). Degradation of zooxanthellae and regulation of their density in hermatypic corals. *Marine Ecology Progress Series*, *139*, 167–178. http://www.int-res.com/articles/meps/139/m139p167.pdf

Webster, N. S., Negri, A. P., Botté, E. S., Laffy, P. W., Flores, F., Noonan, S., Schmidt, C., & Uthicke, S. (2016). Host-associated coral reef microbes respond to the cumulative pressures of ocean warming and ocean acidification. *Scientific Reports*, *6*. https://doi.org/10.1038/srep19324

Webster, N. S., Negri, A. P., Flores, F., Humphrey, C., Soo, R., Botté, E. S., Vogel, N., & Uthicke, S. (2013). Near-future ocean acidification causes differences in microbial associations within diverse coral reef taxa. *Environmental Microbiology Reports*, *5*(2), 243–251. https://doi.org/10.1111/1758-2229.12006

Wiedenmann, J., D’Angelo, C., Mardones, M. L., Moore, S., Benkwitt, C. E., Graham, N. A. J., Hambach, B., Wilson, P. A., Vanstone, J., Eyal, G., Ben-Zvi, O., Loya, Y., & Genin, A. (2023). Reef-building corals farm and feed on their photosynthetic symbionts. *Nature*, *620*(7976), 1018–1024. https://doi.org/10.1038/s41586-023-06442-5

Wilkinson, D. M. (1999). The Disturbing History of Intermediate Disturbance. *Oikos*, *84*(1), 145. https://doi.org/10.2307/3546874

Willis, A. D. (2019). Rarefaction, Alpha Diversity, and Statistics. *Frontiers in Microbiology*, *10*(OCT), 492464. https://doi.org/10.3389/fmicb.2019.02407

Xu, S., Zhan, L., Tang, W., Wang, Q., Dai, Z., Zhou, L., Feng, T., Chen, M., Wu, T., Hu, E., & Yu, G. (2023). MicrobiotaProcess: A comprehensive R package for deep mining microbiome. *Innovation*, *4*(2), 100388. https://doi.org/10.1016/j.xinn.2023.100388

Yamamoto, S., Kayanne, H., Terai, M., Watanabe, A., Kato, K., Negishi, A., & Nozaki, K.

(2012). Threshold of carbonate saturation state determined by CO 2 control experiment. *Biogeosciences*, *9*(4), 1441–1450. https://doi.org/10.5194/bg-9-1441-2012

Yarza, P., Yilmaz, P., Pruesse, E., Glöckner, F. O., Ludwig, W., Schleifer, K. H., Whitman, W. B., Euzéby, J., Amann, R., & Rosselló-Móra, R. (2014). Uniting the classification of cultured and uncultured bacteria and archaea using 16S rRNA gene sequences. *Nature Reviews Microbiology*, *12*(9), 635–645. https://doi.org/10.1038/nrmicro3330

Yong, H. L., Mustapa, N. I., Lee, L. K., Lim, Z. F., Tan, T. H., Usup, G., Gu, H., Litaker, R. W., Tester, P. A., Lim, P. T., & Leaw, C. P. (2018). Habitat complexity affects benthic harmful dinoflagellate assemblages in the fringing reef of Rawa Island, Malaysia. *Harmful Algae*, *78*, 56–68. https://doi.org/10.1016/j.hal.2018.07.009

Ziegler, M., Seneca, F. O., Yum, L. K., Palumbi, S. R., & Voolstra, C. R. (2017). Bacterial community dynamics are linked to patterns of coral heat tolerance. *Nature Communications*, *8*(1), 1–8. https://doi.org/10.1038/ncomms14213

ANNEX 1. Seawater DNA extraction

Modified protocol of the DNeasy 96 Blood & Tissue Kit for seawater DNA extraction.

1. Add sterile glass beads to each 1.5 mL tube containing ATL buffer and add 50 uL of Proteinase-K solution to each tube. Pulverise for 60 s at 30 Hz using the TissueLyser II.
2. Incubate overnight at 37°C on a rocking platform at 300 rpm.
3. Vortex 15 s and centrifuge at 11,000 x g for 1 minute.
4. Transfer lysis solution of 96 samples (including negatives) to a sterile 96 deep-well plate (2mL) sealable.
5. Add 1127.5 µl premixed Buffer AL–ethanol to each sample.
   Note: A white precipitate may form upon addition of Buffer AL–ethanol to the lysate. It is important to apply all of the lysate, including the precipitate, to the DNeasy 96 plate in step 8.
6. Ensure that the plate is properly sealed to avoid leakage during shaking. Place a clear cover over the plate and shake the plate vigorously up and down for 15 s. To collect any solution from the seal, centrifuge the plate. Allow the centrifuge to reach 3000 rpm, and then stop the centrifuge. Do not prolong this step.
7. Place two DNeasy 96 plates on top of S-Blocks (provided). Mark the DNeasy 96 plates for later sample identification.
8. Remove and discard the seal from the plate. Carefully transfer the lysate (maximum 900 µl) of each sample from step 6 to each well of the DNeasy 96 plates. Take care not to wet the rims of the wells to avoid aerosols during centrifugation. Do not transfer more than 900 µl per well.
   Note: If the volume of Proteinase K–Buffer ATL working solution was increased in step 5, transfer no more than 900 µl of the supernatant from step 6 to the DNeasy 96 plate.
9. Seal each DNeasy 96 plate with an AirPore Tape Sheet (provided). Centrifuge for 10 min at 6000 rpm.
10. Repeat steps 5 to 9 to pass the rest of the lysate (maximum 900 uL).
11. Remove the tape. Carefully add 500 µl Buffer AW1 to each sample.
12. Seal each DNeasy 96 plate with a new AirPore Tape Sheet (provided). Centrifuge for 5 min at 6000 rpm.
13. Remove the tape. Carefully add 500 µl Buffer AW2 to each sample.
14. Centrifuge for 15 min at 6000 rpm. Do not seal the plate with AirPore Tape.
15. Place each DNeasy 96 plate in the correct orientation on a new rack of Elution Microtubes RS (provided).
16. To elute the DNA, add 100 µl Buffer AE to each sample, and seal the DNeasy 96 plates with new AirPore Tape Sheets (provided). Incubate for 1 min at room temperature. Centrifuge for 2 min at 6000 rpm.
17. Repeat step 16 using the 100 µl eluate from the first elution.
18. Quantify DNA concentration of each sample to verify for successful extraction and potential contamination. Upload DNA concentrations on the google drive folder and/or indicate the values in the “Extraction-PLATEposition” excel sheet.

ANNEX 2. Substrate DNA extraction

Modified protocol of the NucleoSpin Soil kit for substrate DNA extraction.

Samples processing

1. Process 23 samples at a time and add a negative control in step 10 (total = 24 samples per extraction run).
2. Sterilise a scrapper/spoon and tweezers, by first dipping in bleach, then in milliQ and finally in ethanol 96%. Do not dry with a cloth. Ready to use.
3. If big pieces of corals/algae are present in the sample tube, hold the piece in the tube with the ethanol using the tweezers and scrape the solid surface from all sides to try to detach as many bacteria/algae/sand as possible. Note: if sand, do not touch and pass to the next sample.
4. After scraping, remove the pieces from the tube and keep the ethanol sample for later.
5. Do so with all samples.
6. Transfer 2 mL of ethanol from the sample into a 2 mL tube. Centrifuge at max speed for 20 minutes to precipitate the DNA.
7. Gently remove the supernatant ethanol from the tube.
8. Repeat steps 5-6 until the whole sample is empty.
9. If sediment remains in the original sampling tube, use a spoon/spatula to transfer as much as possible of the sediment into the 2 mL tube.
10. Leave the sample to dry with the lid open in a thermomix at 50°C under the clean bench overnight. Include an empty 2 mL tube with lid open that will serve as negative control for this extraction run.
11. Start the NucleoSpin extraction protocol.

Step 1: Lysis of the sample

1. Transfer the ceramic beads from the NucleoSpin® Bead Tube Type A into the 2 mL tube.
2. Add 700 µL Buffer SL1
3. Add 150 µL Enhancer SX
4. Add 50 µL Proteinase-K and close the cap.
5. Place the 2 mL tubes in the TissueLyser II.
6. Vortex the samples at full speed and room temperature (18–25 °C) for 5 min.
7. Place the 2 mL tubes in a thermomix at 37°C with 300 RPM under the clean bench overnight.

Step 2: Precipitate contaminants

8. Centrifuge for 2 min at 11,000 x g to eliminate the foam caused by the detergent.
9. Transfer the clear supernatant to a new 2 mL tube.
10. Add 150 µL Buffer SL3 and vortex for 5 s.
11. Incubate for 5 min at 0–4 °C (in the fridge).
12. Centrifuge for 1 min at 11,000 x g.

Step 3: Filter lysate, adjust binding condition and bind DNA

Same as official protocol

Step 4: Wash and dry silica membrane

Same as official protocol

Step 5: Elute DNA

30. Place the NucleoSpin® Soil Column into a new 1.5 microcentrifuge tube (not provided).
31. Add 100 µL (for high yield) Buffer SE to the column. Do not close the lid and incubate for 1 min at room temperature (18–25 °C). Close the lid and centrifuge for 30 s at 11,000 x g.
31. Repeat step 31 by pipetting the eluted DNA back onto the column to increase DNA yield.

ANNEX 3: List of ESVs

List of sequenced ESVs after filtering (Data filtering and replicate merging in Methods section). It includes the ESV number and the taxonomic assignment (Taxa). Taxa has been assigned according to cut-off points of the percentage of identity (ID), which are: 98.7% for species, 94.5% for genus, 86.5% for family, 82% for order, 78.5 for class and 75% for phylum (Yarza et al., 2014).

	Domain	Phylum	Class	Order
ESV_11	Bacteria	Proteobacteria	Gammaproteobacteria	Burkholderiales
ESV_15	Bacteria	Proteobacteria	Gammaproteobacteria	Burkholderiales
ESV_18	Bacteria	Proteobacteria	Gammaproteobacteria	Pseudomonadales
ESV_21	Bacteria	Proteobacteria	Alphaproteobacteria	Rhodobacterales
ESV_23	Bacteria	Cyanobacteria	Cyanobacteriia	Synechococcales
ESV_25	Bacteria	Proteobacteria	Gammaproteobacteria	Xanthomonadales
ESV_26	Bacteria	Firmicutes	Bacilli	Staphylococcales
ESV_27	Bacteria	Firmicutes	Bacilli	Lactobacillales
ESV_30	Bacteria	Proteobacteria	Alphaproteobacteria	Rhizobiales
ESV_31	Bacteria	Proteobacteria	Alphaproteobacteria	SAR11clade
ESV_32	Bacteria	Proteobacteria	Gammaproteobacteria	Pseudomonadales
ESV_33	Bacteria	Proteobacteria	Gammaproteobacteria	Pseudomonadales
ESV_35	Bacteria	Proteobacteria	Gammaproteobacteria	Pseudomonadales
ESV_37	Bacteria	Firmicutes	Bacilli	Lactobacillales
ESV_38	Bacteria	Proteobacteria	Alphaproteobacteria	Rhizobiales
ESV_43	Bacteria	Proteobacteria	Alphaproteobacteria	SAR11clade
ESV_45	Bacteria	Actinobacteriota	Actinobacteria	Micrococcales
ESV_46	Bacteria	Proteobacteria	Alphaproteobacteria	SAR11clade
ESV_47	Bacteria	Proteobacteria	Alphaproteobacteria	Rhodobacterales
ESV_48	Bacteria	Proteobacteria	Alphaproteobacteria	Rhodobacterales
ESV_51	Bacteria	Cyanobacteria	Cyanobacteriia	Synechococcales
ESV_52	Bacteria	Proteobacteria	Alphaproteobacteria	Rhodobacterales
ESV_53	Bacteria	Bacteroidota	Bacteroidia	Bacteroidales
ESV_1601	Bacteria	Proteobacteria	Alphaproteobacteria	Rhodospirillales
ESV_1603	Bacteria	Proteobacteria	Alphaproteobacteria	Rhodobacterales
ESV_1611	Bacteria	Bacteroidota	Bacteroidia	Flavobacteriales
ESV_1615	Bacteria	Cyanobacteria	Cyanobacteriia	unclassified
ESV_1617	Bacteria	Proteobacteria	Gammaproteobacteria	Vibrionales
ESV_1622	Bacteria	Bacteroidota	Bacteroidia	Flavobacteriales
ESV_1639	Bacteria	Planctomycetota	Planctomycetes	unclassified
ESV_1640	Bacteria	Proteobacteria	Gammaproteobacteria	Burkholderiales
ESV_1642	Bacteria	Proteobacteria	Alphaproteobacteria	Rhizobiales
ESV_1644	Bacteria	Cyanobacteria	Cyanobacteriia	Cyanobacteriales
ESV_1646	Bacteria	Cyanobacteria	Cyanobacteriia	Cyanobacteriales
ESV_1655	Bacteria	Proteobacteria	Alphaproteobacteria	Rhodobacterales
ESV_1657	Bacteria	Proteobacteria	Alphaproteobacteria	unclassified
ESV_1671	Bacteria	Proteobacteria	Gammaproteobacteria	Oceanospirillales
ESV_1672	Bacteria	Proteobacteria	Gammaproteobacteria	SAR86 clade
ESV_1680	Bacteria	Cyanobacteria	Cyanobacteriia	Phormidesmiales
ESV_1686	Bacteria	Bacteroidota	Bacteroidia	unclassified
ESV_1688	Bacteria	Proteobacteria	Gammaproteobacteria	Burkholderiales
ESV_1695	Archaea	Crenarchaeota	Nitrososphaeria	Nitrosopumilales
ESV_1696	Bacteria	Proteobacteria	Gammaproteobacteria	unclassified
ESV_1705	Bacteria	Firmicutes	Bacilli	unclassified
ESV_1709	Bacteria	Proteobacteria	Gammaproteobacteria	unclassified
ESV_1710	Bacteria	Proteobacteria	Gammaproteobacteria	unclassified

ESV_54	Bacteria	Proteobacteria	Gammaproteobacteria	Pseudomonadales
ESV_55	Bacteria	Proteobacteria	Gammaproteobacteria	Pseudomonadales
ESV_57	Bacteria	Proteobacteria	Gammaproteobacteria	Burkholderiales
ESV_58	Bacteria	Proteobacteria	Alphaproteobacteria	unclassified
ESV_59	Bacteria	Proteobacteria	Gammaproteobacteria	unclassified
ESV_60	Bacteria	Proteobacteria	Gammaproteobacteria	Pseudomonadales
ESV_61	Bacteria	Actinobacteriota	Acidimicrobiia	Actinomarinales
ESV_63	Bacteria	Proteobacteria	Alphaproteobacteria	Rhodobacterales
ESV_64	Bacteria	Proteobacteria	Gammaproteobacteria	Pseudomonadales
ESV_65	Bacteria	Actinobacteriota	Acidimicrobiia	Actinomarinales
ESV_66	Bacteria	Proteobacteria	Alphaproteobacteria	SAR11clade
ESV_67	Bacteria	Actinobacteriota	Actinobacteria	Corynebacteriales
ESV_68	Bacteria	Proteobacteria	Gammaproteobacteria	Burkholderiales
ESV_69	Bacteria	Myxococcota	Myxococcia	Myxococcales
ESV_70	Bacteria	Proteobacteria	Gammaproteobacteria	Alteromonadales
ESV_72	Bacteria	Proteobacteria	Gammaproteobacteria	Pseudomonadales
ESV_73	Bacteria	Actinobacteriota	Actinobacteria	Propionibacteriales
ESV_74	Bacteria	Proteobacteria	Gammaproteobacteria	Alteromonadales
ESV_75	Bacteria	Proteobacteria	Alphaproteobacteria	Rhizobiales
ESV_76	Bacteria	Actinobacteriota	Actinobacteria	Corynebacteriales
ESV_77	Bacteria	Proteobacteria	Alphaproteobacteria	Rhodobacterales
ESV_78	Bacteria	Proteobacteria	Gammaproteobacteria	Burkholderiales
ESV_80	Bacteria	Proteobacteria	Alphaproteobacteria	Sphingomonadales
ESV_82	Bacteria	Firmicutes	Bacilli	Lactobacillales
ESV_85	Bacteria	Proteobacteria	Alphaproteobacteria	Rhodobacterales
ESV_86	Bacteria	Proteobacteria	Gammaproteobacteria	Burkholderiales
ESV_87	Bacteria	Cyanobacteria	Cyanobacteriia	Synechococcales
ESV_88	Bacteria	Proteobacteria	Gammaproteobacteria	Pseudomonadales
ESV_90	Bacteria	Proteobacteria	Alphaproteobacteria	Rhizobiales
ESV_91	Bacteria	Proteobacteria	Gammaproteobacteria	SAR86 clade
ESV_92	Bacteria	Proteobacteria	Alphaproteobacteria	Rhodospirillales
ESV_1718	Bacteria	Firmicutes	Clostridia	Clostridiales
ESV_1724	Bacteria	Cyanobacteria	Cyanobacteriia	Phormidesmiales
ESV_1725	Bacteria	Firmicutes	Clostridia	unclassified
ESV_1726	Bacteria	Bacteroidota	Bacteroidia	Flavobacteriales
ESV_1733	Bacteria	Desulfobacterota	Desulfovibrionia	Desulfovibrionales
ESV_1746	Bacteria	Proteobacteria	Alphaproteobacteria	unclassified
ESV_1753	Bacteria	Proteobacteria	Gammaproteobacteria	Vibrionales
ESV_1758	Bacteria	Acidobacteriota	Holophagae	Acanthopleuribacterales
ESV_1766	Bacteria	Cyanobacteria	Cyanobacteriia	Cyanobacteriales
ESV_1769	Bacteria	Proteobacteria	Gammaproteobacteria	Arenicellales
ESV_1770	Bacteria	Bacteroidota	Bacteroidia	Flavobacteriales
ESV_1771	Bacteria	Proteobacteria	Alphaproteobacteria	Rhodobacterales
ESV_1772	Bacteria	Proteobacteria	Gammaproteobacteria	Steroidobacterales
ESV_1774	Bacteria	Proteobacteria	Alphaproteobacteria	unclassified
ESV_1777	Bacteria	Proteobacteria	Gammaproteobacteria	SAR86 clade
ESV_1785	Bacteria	Proteobacteria	Gammaproteobacteria	Alteromonadales
ESV_1795	Bacteria	Verrucomicrobiota	Lentisphaeria	Lentisphaerales
ESV_1799	Bacteria	Proteobacteria	Alphaproteobacteria	SAR11clade
ESV_1820	Bacteria	Proteobacteria	Gammaproteobacteria	Steroidobacterales
ESV_1821	Bacteria	Proteobacteria	Gammaproteobacteria	Tenderiales
ESV_1822	Bacteria	Bacteroidota	Bacteroidia	Flavobacteriales
ESV_1827	Bacteria	Proteobacteria	Alphaproteobacteria	Rhizobiales
ESV_1830	Bacteria	Bacteroidota	Bacteroidia	Flavobacteriales
ESV_1833	Bacteria	Verrucomicrobiota	Verrucomicrobiae	Arctic97B-4 clade
ESV_1838	Bacteria	Proteobacteria	Alphaproteobacteria	Rhizobiales
ESV_1844	Bacteria	Cyanobacteria	Cyanobacteriia	Cyanobacteriales
ESV_1848	Bacteria	Bacteroidota	Bacteroidia	Flavobacteriales
ESV_1862	Bacteria	Proteobacteria	Gammaproteobacteria	Steroidobacterales
ESV_1863	Bacteria	Bacteroidota	Bacteroidia	unclassified
ESV_1865	Bacteria	Planctomycetota	Planctomycetes	Pirellulales
ESV_1871	Archaea	Crenarchaeota	Nitrososphaeria	Nitrosopumilales

ESV_93	Bacteria	Proteobacteria	Alphaproteobacteria	Puniceispirillales
ESV_94	Bacteria	Bacteroidota	Bacteroidia	Cytophagales
ESV_95	Bacteria	Proteobacteria	Gammaproteobacteria	Xanthomonadales
ESV_96	Bacteria	Myxococcota	Myxococcia	Myxococcales
ESV_97	Bacteria	Bacteroidota	Bacteroidia	Flavobacteriales
ESV_98	Bacteria	Bacteroidota	Bacteroidia	Flavobacteriales
ESV_100	Bacteria	Proteobacteria	Alphaproteobacteria	SAR11clade
ESV_102	Bacteria	Proteobacteria	Gammaproteobacteria	Oceanospirillales
ESV_103	Bacteria	Proteobacteria	Alphaproteobacteria	Rhizobiales
ESV_104	Bacteria	Cyanobacteria	Cyanobacteriia	Synechococcales
ESV_105	Bacteria	Proteobacteria	Alphaproteobacteria	Rhizobiales
ESV_107	Bacteria	Proteobacteria	Alphaproteobacteria	Rhodobacterales
ESV_108	Bacteria	Proteobacteria	Alphaproteobacteria	Rhizobiales
ESV_109	Bacteria	Bacteroidota	Bacteroidia	Flavobacteriales
ESV_111	Bacteria	Proteobacteria	Gammaproteobacteria	Pseudomonadales
ESV_112	Bacteria	Proteobacteria	Gammaproteobacteria	Pseudomonadales
ESV_113	Bacteria	Proteobacteria	Gammaproteobacteria	Pseudomonadales
ESV_114	Bacteria	Proteobacteria	Alphaproteobacteria	Caulobacterales
ESV_115	Bacteria	Proteobacteria	Gammaproteobacteria	Pseudomonadales
ESV_117	Bacteria	Firmicutes	Bacilli	Bacillales
ESV_118	Bacteria	Proteobacteria	Alphaproteobacteria	Rhodobacterales
ESV_122	Bacteria	Proteobacteria	Gammaproteobacteria	SAR86 clade
ESV_123	Bacteria	Proteobacteria	Gammaproteobacteria	Burkholderiales
ESV_124	Bacteria	Proteobacteria	Gammaproteobacteria	SAR86 clade
ESV_125	Bacteria	Cyanobacteria	Cyanobacteriia	Synechococcales
ESV_126	Bacteria	Actinobacteriota	Acidimicrobiia	Actinomarinales
ESV_127	Bacteria	Actinobacteriota	Actinobacteria	Micrococcales
ESV_128	Bacteria	Proteobacteria	Alphaproteobacteria	Sphingomonadales
ESV_129	Bacteria	Bacteroidota	Bacteroidia	Flavobacteriales
ESV_130	Bacteria	Planctomycetota	Planctomycetes	Pirellulales
ESV_131	Bacteria	Proteobacteria	Gammaproteobacteria	Burkholderiales
ESV_1875	Bacteria	Proteobacteria	Gammaproteobacteria	Oceanospirillales
ESV_1885	Bacteria	Proteobacteria	Alphaproteobacteria	Rhizobiales
ESV_1887	Bacteria	Firmicutes	Clostridia	Clostridiales
ESV_1896	Archaea	Crenarchaeota	Nitrososphaeria	Nitrososphaerales
ESV_1906	Bacteria	Proteobacteria	Gammaproteobacteria	Burkholderiales
ESV_1907	Bacteria	Planctomycetota	Planctomycetes	Pirellulales
ESV_1921	Bacteria	Proteobacteria	Alphaproteobacteria	Rhizobiales
ESV_1924	Bacteria	Cyanobacteria	Cyanobacteriia	Cyanobacteriales
ESV_1926	Bacteria	Proteobacteria	Alphaproteobacteria	Rhodobacterales
ESV_1928	Bacteria	Actinobacteriota	Thermoleophilia	Solirubrobacterales
ESV_1934	Bacteria	Proteobacteria	Alphaproteobacteria	Rhizobiales
ESV_1941	Bacteria	Bacteroidota	Bacteroidia	unclassified
ESV_1946	Bacteria	Verrucomicrobiota	Verrucomicrobiae	Opitutales
ESV_1949	Bacteria	Proteobacteria	Alphaproteobacteria	Rhizobiales
ESV_1951	Bacteria	Proteobacteria	Alphaproteobacteria	Acetobacterales
ESV_1958	Bacteria	Firmicutes	Clostridia	Clostridiales
ESV_1962	Bacteria	Planctomycetota	Planctomycetes	Pirellulales
ESV_1964	Bacteria	Proteobacteria	Alphaproteobacteria	Rhodobacterales
ESV_1971	Bacteria	Planctomycetota	Planctomycetes	Pirellulales
ESV_1973	Bacteria	Planctomycetota	Planctomycetes	Pirellulales
ESV_1979	Bacteria	Bacteroidota	Bacteroidia	Flavobacteriales
ESV_1986	Bacteria	Bacteroidota	Bacteroidia	Flavobacteriales
ESV_1989	Bacteria	Proteobacteria	Gammaproteobacteria	SAR86 clade
ESV_1996	Archaea	Crenarchaeota	Nitrososphaeria	Nitrosopumilales
ESV_1997	Bacteria	Proteobacteria	Gammaproteobacteria	Alteromonadales
ESV_2007	Bacteria	Proteobacteria	Gammaproteobacteria	Nitrosococcales
ESV_2008	Bacteria	Proteobacteria	Alphaproteobacteria	Parvibaculales
ESV_2010	Bacteria	Cyanobacteria	Cyanobacteriia	Phormidesmiales
ESV_2015	Bacteria	Proteobacteria	Gammaproteobacteria	Alteromonadales
ESV_2020	Bacteria	Cyanobacteria	Cyanobacteriia	Cyanobacteriales
ESV_2030	Bacteria	Verrucomicrobiota	Verrucomicrobiae	Verrucomicrobiales

ESV_135	Bacteria	Proteobacteria	Alphaproteobacteria	Kiloniellales
ESV_136	Bacteria	Proteobacteria	Alphaproteobacteria	SAR11clade
ESV_138	Bacteria	Bacteroidota	Bacteroidia	Flavobacteriales
ESV_139	Bacteria	Proteobacteria	Alphaproteobacteria	Rhizobiales
ESV_140	Bacteria	Proteobacteria	Alphaproteobacteria	Rhizobiales
ESV_142	Bacteria	Proteobacteria	Gammaproteobacteria	Burkholderiales
ESV_143	Bacteria	Proteobacteria	Alphaproteobacteria	Rhodobacterales
ESV_145	Bacteria	Proteobacteria	Gammaproteobacteria	Burkholderiales
ESV_151	Bacteria	Firmicutes	Bacilli	Staphylococcales
ESV_152	Bacteria	Proteobacteria	Alphaproteobacteria	SAR11clade
ESV_153	Bacteria	Proteobacteria	Gammaproteobacteria	SAR86 clade
ESV_154	Bacteria	Proteobacteria	Gammaproteobacteria	Pseudomonadales
ESV_155	Bacteria	Proteobacteria	Alphaproteobacteria	Rhizobiales
ESV_156	Bacteria	Proteobacteria	Alphaproteobacteria	Sphingomonadales
ESV_157	Bacteria	Actinobacteriota	Acidimicrobiia	Microtrichales
ESV_158	Bacteria	Proteobacteria	Gammaproteobacteria	Pseudomonadales
ESV_160	Bacteria	Proteobacteria	Gammaproteobacteria	Alteromonadales
ESV_161	Bacteria	Proteobacteria	Alphaproteobacteria	Rhodobacterales
ESV_162	Bacteria	Proteobacteria	Alphaproteobacteria	Rhodobacterales
ESV_166	Bacteria	Bacteroidota	Bacteroidia	Flavobacteriales
ESV_167	Bacteria	Proteobacteria	Alphaproteobacteria	Kiloniellales
ESV_168	Bacteria	Cyanobacteria	Cyanobacteriia	Cyanobacteriales
ESV_169	Bacteria	Bacteroidota	Bacteroidia	Flavobacteriales
ESV_170	Bacteria	Proteobacteria	Gammaproteobacteria	Burkholderiales
ESV_171	Bacteria	Proteobacteria	Gammaproteobacteria	Cellvibrionales
ESV_173	Bacteria	Desulfobacterota	Desulfobacteria	Desulfobacterales
ESV_174	Bacteria	Proteobacteria	Gammaproteobacteria	Cellvibrionales
ESV_175	Bacteria	Proteobacteria	Gammaproteobacteria	unclassified
ESV_176	Bacteria	Firmicutes	Clostridia	Lachnospirales
ESV_177	Bacteria	Proteobacteria	Gammaproteobacteria	Steroidobacterales
ESV_178	Bacteria	Planctomycetota	Planctomycetes	Pirellulales
ESV_2031	Bacteria	Proteobacteria	Gammaproteobacteria	unclassified
ESV_2032	Bacteria	Proteobacteria	Alphaproteobacteria	unclassified
ESV_2033	Bacteria	Cyanobacteria	Cyanobacteriia	Cyanobacteriales
ESV_2042	Bacteria	Proteobacteria	Gammaproteobacteria	unclassified
ESV_2047	Bacteria	Cyanobacteria	Cyanobacteriia	Cyanobacteriales
ESV_2053	Bacteria	Proteobacteria	Gammaproteobacteria	Alteromonadales
ESV_2055	Bacteria	Bacteroidota	Bacteroidia	Cytophagales
ESV_2062	Bacteria	Proteobacteria	Gammaproteobacteria	unclassified
ESV_2069	Bacteria	Actinobacteriota	Actinobacteria	Corynebacteriales
ESV_2072	Bacteria	Verrucomicrobiota	Lentisphaeria	Lentisphaerales
ESV_2075	Bacteria	Planctomycetota	Planctomycetes	Pirellulales
ESV_2086	Bacteria	Verrucomicrobiota	Verrucomicrobiae	Opitutales
ESV_2088	Bacteria	Proteobacteria	Alphaproteobacteria	unclassified
ESV_2089	Bacteria	Actinobacteriota	Actinobacteria	Bifidobacteriales
ESV_2093	Bacteria	Proteobacteria	Alphaproteobacteria	Rickettsiales
ESV_2102	Bacteria	Firmicutes	Clostridia	Clostridiales
ESV_2105	Bacteria	Proteobacteria	Gammaproteobacteria	unclassified
ESV_2110	Bacteria	Bacteroidota	Rhodothermia	Balneolales
ESV_2118	Bacteria	Bacteroidota	Bacteroidia	Flavobacteriales
ESV_2119	Bacteria	Cyanobacteria	Cyanobacteriia	Cyanobacteriales
ESV_2120	Bacteria	Planctomycetota	Planctomycetes	Pirellulales
ESV_2135	Bacteria	Bacteroidota	Bacteroidia	Flavobacteriales
ESV_2140	Bacteria	Proteobacteria	Gammaproteobacteria	Cellvibrionales
ESV_2141	Bacteria	Proteobacteria	Alphaproteobacteria	unclassified
ESV_2143	Bacteria	Bacteroidota	Bacteroidia	Flavobacteriales
ESV_2161	Bacteria	Proteobacteria	Gammaproteobacteria	Oceanospirillales
ESV_2166	Bacteria	Bacteroidota	Bacteroidia	Flavobacteriales
ESV_2167	Bacteria	Acidobacteriota	Thermoanaerobaculia	Thermoanaerobaculales
ESV_2171	Bacteria	Proteobacteria	Gammaproteobacteria	unclassified
ESV_2187	Bacteria	Proteobacteria	Alphaproteobacteria	Rickettsiales
ESV_2194	Bacteria	Proteobacteria	Alphaproteobacteria	Rhodobacterales

ESV_183	Bacteria	Bacteroidota	Bacteroidia	Bacteroidales
ESV_184	Bacteria	Proteobacteria	Alphaproteobacteria	Kiloniellales
ESV_188	Bacteria	Actinobacteriota	Actinobacteria	Corynebacteriales
ESV_190	Bacteria	Proteobacteria	Alphaproteobacteria	Rhizobiales
ESV_193	Bacteria	Firmicutes	Bacilli	Lactobacillales
ESV_194	Bacteria	Firmicutes	Bacilli	Lactobacillales
ESV_195	Bacteria	Proteobacteria	Alphaproteobacteria	SAR11clade
ESV_196	Bacteria	Actinobacteriota	Acidimicrobiia	Microtrichales
ESV_198	Bacteria	Proteobacteria	Alphaproteobacteria	Rhodospirillales
ESV_199	Bacteria	Bacteroidota	Bacteroidia	Flavobacteriales
ESV_200	Bacteria	Planctomycetota	Planctomycetes	Pirellulales
ESV_202	Bacteria	Proteobacteria	Alphaproteobacteria	Caulobacterales
ESV_204	Bacteria	Proteobacteria	Gammaproteobacteria	SAR86 clade
ESV_208	Bacteria	Proteobacteria	Alphaproteobacteria	Caulobacterales
ESV_209	Bacteria	Proteobacteria	Alphaproteobacteria	Rhodobacterales
ESV_210	Bacteria	Firmicutes	Clostridia	Tissierellales
ESV_212	Bacteria	Proteobacteria	Alphaproteobacteria	Rhodobacterales
ESV_214	Bacteria	Cyanobacteria	Cyanobacteriia	Eurycoccales
ESV_215	Bacteria	Proteobacteria	Gammaproteobacteria	Burkholderiales
ESV_216	Bacteria	Bacteroidota	Bacteroidia	Flavobacteriales
ESV_218	Bacteria	Proteobacteria	Alphaproteobacteria	unclassified
ESV_219	Bacteria	Firmicutes	Bacilli	Lactobacillales
ESV_220	Bacteria	Proteobacteria	Gammaproteobacteria	Pseudomonadales
ESV_223	Bacteria	Proteobacteria	Gammaproteobacteria	Burkholderiales
ESV_224	Bacteria	Proteobacteria	Alphaproteobacteria	Sphingomonadales
ESV_226	Bacteria	Proteobacteria	Alphaproteobacteria	Rhodobacterales
ESV_233	Bacteria	Firmicutes	Clostridia	Tissierellales
ESV_234	Bacteria	Planctomycetota	Phycisphaerae	Phycisphaerales
ESV_235	Bacteria	Proteobacteria	Alphaproteobacteria	SAR11clade
ESV_236	Bacteria	Planctomycetota	Planctomycetes	Pirellulales
ESV_239	Bacteria	Proteobacteria	Alphaproteobacteria	Rhizobiales
ESV_2196	Bacteria	Proteobacteria	Alphaproteobacteria	Rhizobiales
ESV_2205	Bacteria	Proteobacteria	Alphaproteobacteria	Rhizobiales
ESV_2207	Bacteria	Verrucomicrobiota	Verrucomicrobiae	unclassified
ESV_2208	Bacteria	Firmicutes	Clostridia	Lachnospirales
ESV_2213	Bacteria	Cyanobacteria	Cyanobacteriia	unclassified
ESV_2215	Archaea	Crenarchaeota	Nitrososphaeria	Nitrosopumilales
ESV_2216	Archaea	Crenarchaeota	Nitrososphaeria	Nitrosopumilales
ESV_2218	Archaea	Crenarchaeota	Nitrososphaeria	Nitrosopumilales
ESV_2219	Bacteria	Proteobacteria	Gammaproteobacteria	Burkholderiales
ESV_2220	Bacteria	Proteobacteria	Gammaproteobacteria	SAR86 clade
ESV_2231	Bacteria	Proteobacteria	Alphaproteobacteria	SAR11clade
ESV_2240	Archaea	Thermoplasmatota	Thermoplasmata	unclassified
ESV_2242	Bacteria	Verrucomicrobiota	Verrucomicrobiae	Verrucomicrobiales
ESV_2248	Bacteria	Proteobacteria	Gammaproteobacteria	Steroidobacterales
ESV_2253	Bacteria	Proteobacteria	Gammaproteobacteria	Pseudomonadales
ESV_2255	Bacteria	Actinobacteriota	Actinobacteria	Propionibacteriales
ESV_2263	Archaea	Crenarchaeota	Nitrososphaeria	Nitrosopumilales
ESV_2266	Bacteria	Proteobacteria	Alphaproteobacteria	Rhodospirillales
ESV_2270	Bacteria	Bacteroidota	Bacteroidia	Flavobacteriales
ESV_2277	Bacteria	Bacteroidota	Bacteroidia	Flavobacteriales
ESV_2282	Bacteria	Proteobacteria	Alphaproteobacteria	Rickettsiales
ESV_2286	Bacteria	Proteobacteria	Gammaproteobacteria	Cellvibrionales
ESV_2289	Bacteria	Proteobacteria	Alphaproteobacteria	Rhodobacterales
ESV_2297	Bacteria	Proteobacteria	Gammaproteobacteria	Cellvibrionales
ESV_2303	Bacteria	Proteobacteria	Alphaproteobacteria	Rhodobacterales
ESV_2304	Bacteria	Cyanobacteria	Cyanobacteriia	Cyanobacteriales
ESV_2312	Archaea	Thermoplasmatota	Thermoplasmata	unclassified
ESV_2313	Bacteria	Cyanobacteria	Cyanobacteriia	Cyanobacteriales
ESV_2320	Bacteria	Proteobacteria	Alphaproteobacteria	SAR11clade
ESV_2322	Bacteria	Proteobacteria	Gammaproteobacteria	KI89A clade
ESV_2324	Bacteria	Proteobacteria	Alphaproteobacteria	SAR11clade

ESV_242	Bacteria	Bacteroidota	Bacteroidia	Chitinophagales
ESV_243	Bacteria	Dadabacteria	Dadabacteriia	Dadabacteriales
ESV_245	Bacteria	Firmicutes	Clostridia	Clostridiales
ESV_246	Bacteria	Proteobacteria	Alphaproteobacteria	Kiloniellales
ESV_247	Bacteria	Bacteroidota	Bacteroidia	Flavobacteriales
ESV_249	Bacteria	Proteobacteria	Gammaproteobacteria	Cellvibrionales
ESV_251	Bacteria	Proteobacteria	Alphaproteobacteria	Rhizobiales
ESV_252	Bacteria	Planctomycetota	Planctomycetes	Pirellulales
ESV_254	Bacteria	Proteobacteria	Alphaproteobacteria	Rhizobiales
ESV_256	Bacteria	Proteobacteria	Gammaproteobacteria	Vibrionales
ESV_258	Bacteria	Actinobacteriota	Actinobacteria	Micrococcales
ESV_259	Bacteria	Bacteroidota	Bacteroidia	Bacteroidales
ESV_262	Bacteria	Cyanobacteria	Cyanobacteriia	Eurycoccales
ESV_264	Bacteria	Proteobacteria	Alphaproteobacteria	Rhizobiales
ESV_266	Bacteria	Proteobacteria	Gammaproteobacteria	Burkholderiales
ESV_267	Bacteria	Planctomycetota	Planctomycetes	Pirellulales
ESV_268	Bacteria	Bacteroidota	Bacteroidia	unclassified
ESV_270	Bacteria	Proteobacteria	Alphaproteobacteria	unclassified
ESV_274	Bacteria	Proteobacteria	Alphaproteobacteria	unclassified
ESV_276	Bacteria	Planctomycetota	Planctomycetes	Pirellulales
ESV_279	Bacteria	Proteobacteria	Gammaproteobacteria	Alteromonadales
ESV_280	Bacteria	Proteobacteria	Alphaproteobacteria	unclassified
ESV_281	Bacteria	Planctomycetota	Phycisphaerae	Phycisphaerales
ESV_283	Bacteria	Proteobacteria	Alphaproteobacteria	Rhizobiales
ESV_284	Bacteria	Firmicutes	Bacilli	Staphylococcales
ESV_285	Bacteria	Proteobacteria	Alphaproteobacteria	Rhizobiales
ESV_287	Bacteria	Proteobacteria	Alphaproteobacteria	Rhodobacterales
ESV_288	Bacteria	Firmicutes	Thermoanaerobacteria	Thermoanaerobacterales
ESV_289	Bacteria	Firmicutes	Clostridia	Tissierellales
ESV_290	Bacteria	Proteobacteria	Alphaproteobacteria	Rhodobacterales
ESV_291	Bacteria	Proteobacteria	Alphaproteobacteria	Rhodobacterales
ESV_2335	Bacteria	Proteobacteria	Alphaproteobacteria	unclassified
ESV_2336	Bacteria	Proteobacteria	Gammaproteobacteria	Cellvibrionales
ESV_2343	Bacteria	Planctomycetota	Phycisphaerae	Phycisphaerales
ESV_2362	Bacteria	Proteobacteria	Alphaproteobacteria	Caulobacterales
ESV_2368	Bacteria	Proteobacteria	Gammaproteobacteria	Nitrosococcales
ESV_2373	Bacteria	Proteobacteria	Gammaproteobacteria	Alteromonadales
ESV_2374	Bacteria	Proteobacteria	Gammaproteobacteria	Nitrosococcales
ESV_2381	Bacteria	Bacteroidota	Bacteroidia	Flavobacteriales
ESV_2384	Bacteria	Cyanobacteria	Cyanobacteriia	Cyanobacteriales
ESV_2388	Bacteria	Proteobacteria	Alphaproteobacteria	Rhodospirillales
ESV_2394	Bacteria	Cyanobacteria	Cyanobacteriia	Cyanobacteriales
ESV_2405	Bacteria	Proteobacteria	Alphaproteobacteria	SAR11clade
ESV_2407	Bacteria	Proteobacteria	Alphaproteobacteria	Rhizobiales
ESV_2417	Bacteria	Proteobacteria	Gammaproteobacteria	Pseudomonadales
ESV_2418	Bacteria	Proteobacteria	Alphaproteobacteria	Rhodobacterales
ESV_2422	Bacteria	Proteobacteria	Alphaproteobacteria	Rickettsiales
ESV_2433	Bacteria	Bacteroidota	Bacteroidia	Flavobacteriales
ESV_2436	Bacteria	Proteobacteria	Gammaproteobacteria	unclassified
ESV_2440	Bacteria	Proteobacteria	Alphaproteobacteria	SAR11clade
ESV_2442	Bacteria	Cyanobacteria	Cyanobacteriia	Phormidesmiales
ESV_2446	Bacteria	Proteobacteria	Gammaproteobacteria	Vibrionales
ESV_2448	Bacteria	Proteobacteria	Gammaproteobacteria	unclassified
ESV_2463	Bacteria	Proteobacteria	Gammaproteobacteria	Vibrionales
ESV_2467	Bacteria	Verrucomicrobiota	Verrucomicrobiae	Opitutales
ESV_2470	Bacteria	Planctomycetota	Planctomycetes	Pirellulales
ESV_2473	Bacteria	Cyanobacteria	Cyanobacteriia	Phormidesmiales
ESV_2475	Bacteria	Bacteroidota	Bacteroidia	Flavobacteriales
ESV_2483	Bacteria	Proteobacteria	Alphaproteobacteria	unclassified
ESV_2486	Bacteria	Cyanobacteria	Cyanobacteriia	unclassified
ESV_2495	Bacteria	Proteobacteria	Alphaproteobacteria	Kiloniellales
ESV_2497	Bacteria	Proteobacteria	Gammaproteobacteria	Oceanospirillales

ESV_293	Bacteria	Proteobacteria	Gammaproteobacteria	unclassified
ESV_294	Bacteria	Bacteroidota	Bacteroidia	Flavobacteriales
ESV_296	Bacteria	Proteobacteria	Alphaproteobacteria	Kiloniellales
ESV_297	Bacteria	Cyanobacteria	Cyanobacteriia	Cyanobacteriales
ESV_299	Bacteria	Firmicutes	Bacilli	Lactobacillales
ESV_300	Bacteria	Nitrospirota	Nitrospiria	Nitrospirales
ESV_301	Bacteria	Proteobacteria	Alphaproteobacteria	unclassified
ESV_303	Bacteria	Bacteroidota	Bacteroidia	Cytophagales
ESV_304	Bacteria	Proteobacteria	Alphaproteobacteria	Rickettsiales
ESV_306	Bacteria	Proteobacteria	Alphaproteobacteria	Rhodobacterales
ESV_307	Bacteria	Proteobacteria	Alphaproteobacteria	SAR11clade
ESV_312	Bacteria	Bacteroidota	Bacteroidia	unclassified
ESV_313	Bacteria	Proteobacteria	Gammaproteobacteria	unclassified
ESV_314	Bacteria	Proteobacteria	Gammaproteobacteria	unclassified
ESV_316	Bacteria	Proteobacteria	Gammaproteobacteria	unclassified
ESV_317	Bacteria	Proteobacteria	Alphaproteobacteria	Rhizobiales
ESV_318	Bacteria	Verrucomicrobiota	Verrucomicrobiae	Opitutales
ESV_319	Bacteria	Proteobacteria	Alphaproteobacteria	Rhizobiales
ESV_321	Bacteria	Proteobacteria	Alphaproteobacteria	Parvibaculales
ESV_322	Bacteria	Cyanobacteria	Cyanobacteriia	Cyanobacteriales
ESV_323	Bacteria	Firmicutes	Clostridia	Tissierellales
ESV_326	Bacteria	Proteobacteria	Gammaproteobacteria	Burkholderiales
ESV_329	Bacteria	Planctomycetota	Planctomycetes	Pirellulales
ESV_330	Bacteria	Proteobacteria	Alphaproteobacteria	Rickettsiales
ESV_331	Bacteria	Bacteroidota	Bacteroidia	Flavobacteriales
ESV_334	Bacteria	Proteobacteria	Alphaproteobacteria	Parvibaculales
ESV_336	Bacteria	Bacteroidota	Bacteroidia	Flavobacteriales
ESV_337	Bacteria	Proteobacteria	Alphaproteobacteria	Rhizobiales
ESV_339	Bacteria	Cyanobacteria	Cyanobacteriia	Cyanobacteriales
ESV_341	Bacteria	Planctomycetota	Planctomycetes	Pirellulales
ESV_342	Bacteria	Bacteroidota	Bacteroidia	Flavobacteriales
ESV_2507	Bacteria	Cyanobacteria	Cyanobacteriia	unclassified
ESV_2510	Bacteria	Proteobacteria	Alphaproteobacteria	Rhodospirillales
ESV_2514	Bacteria	Verrucomicrobiota	Verrucomicrobiae	Pedosphaerales
ESV_2517	Bacteria	Proteobacteria	Alphaproteobacteria	Rickettsiales
ESV_2518	Bacteria	Firmicutes	Clostridia	Lachnospirales
ESV_2528	Bacteria	Bdellovibrionota	Oligoflexia	Oligoflexales
ESV_2531	Bacteria	Planctomycetota	Planctomycetes	Pirellulales
ESV_2532	Bacteria	Verrucomicrobiota	Lentisphaeria	Lentisphaerales
ESV_2534	Bacteria	Actinobacteriota	Actinobacteria	unclassified
ESV_2537	Bacteria	Verrucomicrobiota	Verrucomicrobiae	Verrucomicrobiales
ESV_2544	Bacteria	Proteobacteria	Gammaproteobacteria	OM182 clade
ESV_2551	Archaea	Thermoplasmatota	Thermoplasmata	unclassified
ESV_2563	Bacteria	Verrucomicrobiota	Lentisphaeria	Lentisphaerales
ESV_2571	Bacteria	Proteobacteria	Gammaproteobacteria	Vibrionales
ESV_2583	Bacteria	Bacteroidota	Bacteroidia	unclassified
ESV_2586	Bacteria	Proteobacteria	Alphaproteobacteria	unclassified
ESV_2589	Bacteria	Proteobacteria	Gammaproteobacteria	unclassified
ESV_2595	Bacteria	Actinobacteriota	Rubrobacteria	Rubrobacterales
ESV_2601	Bacteria	Planctomycetota	Planctomycetes	Planctomycetales
ESV_2607	Bacteria	Planctomycetota	Planctomycetes	Pirellulales
ESV_2609	Bacteria	Proteobacteria	Gammaproteobacteria	Steroidobacterales
ESV_2624	Bacteria	Verrucomicrobiota	Chlamydiae	Chlamydiales
ESV_2625	Bacteria	Planctomycetota	Planctomycetes	Pirellulales
ESV_2639	Bacteria	Bdellovibrionota	Oligoflexia	Oligoflexales
ESV_2645	Bacteria	Proteobacteria	Gammaproteobacteria	Nitrosococcales
ESV_2646	Bacteria	Proteobacteria	Gammaproteobacteria	Steroidobacterales
ESV_2651	Bacteria	Nitrospirota	Nitrospiria	Nitrospirales
ESV_2654	Bacteria	Proteobacteria	Gammaproteobacteria	KI89A clade
ESV_2659	Bacteria	Proteobacteria	Alphaproteobacteria	Rhodobacterales
ESV_2676	Bacteria	Cyanobacteria	Cyanobacteriia	unclassified
ESV_2684	Bacteria	Bacteroidota	Bacteroidia	Flavobacteriales

ESV_343	Bacteria	Proteobacteria	Alphaproteobacteria	Rhodospirillales
ESV_344	Bacteria	Proteobacteria	Alphaproteobacteria	Rhodobacterales
ESV_348	Bacteria	Proteobacteria	Gammaproteobacteria	Enterobacterales
ESV_349	Bacteria	Actinobacteriota	Actinobacteria	Micrococcales
ESV_352	Archaea	Thermoplasmatota	Thermoplasmata	unclassified
ESV_353	Bacteria	Firmicutes	Negativicutes	Veillonellales-Selenomonadales
ESV_357	Bacteria	Proteobacteria	Gammaproteobacteria	unclassified
ESV_358	Bacteria	Proteobacteria	Alphaproteobacteria	SAR11clade
ESV_359	Bacteria	Proteobacteria	Alphaproteobacteria	Puniceispirillales
ESV_361	Bacteria	Proteobacteria	Gammaproteobacteria	Alteromonadales
ESV_362	Bacteria	Proteobacteria	Alphaproteobacteria	Rhizobiales
ESV_363	Bacteria	Proteobacteria	Alphaproteobacteria	Kiloniellales
ESV_364	Bacteria	Proteobacteria	Alphaproteobacteria	Rhizobiales
ESV_365	Bacteria	Planctomycetota	Planctomycetes	Pirellulales
ESV_366	Bacteria	Proteobacteria	Gammaproteobacteria	Enterobacterales
ESV_367	Bacteria	Proteobacteria	Gammaproteobacteria	Cellvibrionales
ESV_369	Bacteria	Cyanobacteria	Cyanobacteriia	Synechococcales
ESV_370	Bacteria	Bacteroidota	Bacteroidia	Cytophagales
ESV_372	Bacteria	Actinobacteriota	Acidimicrobiia	Microtrichales
ESV_373	Bacteria	Proteobacteria	Gammaproteobacteria	Alteromonadales
ESV_374	Bacteria	Proteobacteria	Alphaproteobacteria	SAR11clade
ESV_377	Bacteria	Bacteroidota	Bacteroidia	Flavobacteriales
ESV_378	Bacteria	Proteobacteria	Alphaproteobacteria	Rhodobacterales
ESV_380	Bacteria	Proteobacteria	Gammaproteobacteria	unclassified
ESV_381	Bacteria	Planctomycetota	Planctomycetes	Pirellulales
ESV_383	Bacteria	Planctomycetota	Planctomycetes	Pirellulales
ESV_385	Bacteria	Actinobacteriota	Actinobacteria	Corynebacteriales
ESV_387	Bacteria	Verrucomicrobiota	Kiritimatiellae	Kiritimatiellales
ESV_388	Bacteria	Proteobacteria	Alphaproteobacteria	Rhizobiales
ESV_389	Bacteria	Proteobacteria	Gammaproteobacteria	Vibrionales
ESV_390	Bacteria	Proteobacteria	Alphaproteobacteria	SAR11clade
ESV_2686	Bacteria	Proteobacteria	Alphaproteobacteria	unclassified
ESV_2692	Bacteria	Bacteroidota	Bacteroidia	Flavobacteriales
ESV_2696	Bacteria	Proteobacteria	Gammaproteobacteria	Burkholderiales
ESV_2698	Bacteria	Bacteroidota	Bacteroidia	Flavobacteriales
ESV_2702	Bacteria	Planctomycetota	Planctomycetes	Pirellulales
ESV_2709	Bacteria	Firmicutes	Clostridia	Tissierellales
ESV_2719	Bacteria	Proteobacteria	Alphaproteobacteria	Rhodobacterales
ESV_2731	Bacteria	Bacteroidota	Bacteroidia	Cytophagales
ESV_2738	Archaea	Thermoplasmatota	Thermoplasmata	unclassified
ESV_2760	Bacteria	Proteobacteria	Alphaproteobacteria	Rhodobacterales
ESV_2766	Bacteria	Proteobacteria	Gammaproteobacteria	Pseudomonadales
ESV_2767	Bacteria	Firmicutes	Clostridia	Lachnospirales
ESV_2803	Bacteria	Bacteroidota	Bacteroidia	Cytophagales
ESV_2805	Bacteria	Proteobacteria	Alphaproteobacteria	Parvibaculales
ESV_2815	Bacteria	Actinobacteriota	Acidimicrobiia	Microtrichales
ESV_2821	Bacteria	Cyanobacteria	Cyanobacteriia	Phormidesmiales
ESV_2832	Bacteria	Proteobacteria	Alphaproteobacteria	Rhizobiales
ESV_2839	Bacteria	Proteobacteria	Gammaproteobacteria	Nitrosococcales
ESV_2842	Bacteria	Proteobacteria	Gammaproteobacteria	unclassified
ESV_2843	Bacteria	Proteobacteria	Gammaproteobacteria	Oceanospirillales
ESV_2846	Bacteria	Bacteroidota	Bacteroidia	Flavobacteriales
ESV_2850	Bacteria	Proteobacteria	Gammaproteobacteria	Nitrosococcales
ESV_2858	Bacteria	Verrucomicrobiota	Verrucomicrobiae	Arctic97B-4 clade
ESV_2874	Bacteria	Proteobacteria	Gammaproteobacteria	Burkholderiales
ESV_2884	Bacteria	Proteobacteria	Alphaproteobacteria	SAR11clade
ESV_2889	Bacteria	Proteobacteria	Alphaproteobacteria	Rhodospirillales
ESV_2902	Bacteria	Chloroflexi	Dehalococcoidia	SAR202 clade
ESV_2904	Bacteria	Proteobacteria	Gammaproteobacteria	unclassified
ESV_2915	Bacteria	Firmicutes	Bacilli	Lactobacillales
ESV_2923	Bacteria	Verrucomicrobiota	Verrucomicrobiae	Opitutales
ESV_2934	Bacteria	Proteobacteria	Alphaproteobacteria	Rickettsiales

ESV_391	Bacteria	Proteobacteria	Gammaproteobacteria	Cellvibrionales
ESV_393	Bacteria	Proteobacteria	Gammaproteobacteria	Xanthomonadales
ESV_394	Bacteria	Proteobacteria	Gammaproteobacteria	unclassified
ESV_395	Bacteria	Proteobacteria	Alphaproteobacteria	Rhizobiales
ESV_396	Bacteria	Proteobacteria	Alphaproteobacteria	SAR11clade
ESV_397	Bacteria	Bacteroidota	Bacteroidia	Flavobacteriales
ESV_398	Bacteria	Cyanobacteria	Cyanobacteriia	unclassified
ESV_399	Bacteria	Bacteroidota	Bacteroidia	Flavobacteriales
ESV_400	Bacteria	Proteobacteria	Gammaproteobacteria	SAR86 clade
ESV_401	Bacteria	Bacteroidota	Bacteroidia	Flavobacteriales
ESV_402	Bacteria	Actinobacteriota	Actinobacteria	Bifidobacteriales
ESV_403	Bacteria	Proteobacteria	Alphaproteobacteria	unclassified
ESV_406	Bacteria	Proteobacteria	Alphaproteobacteria	Sphingomonadales
ESV_407	Bacteria	Bacteroidota	Bacteroidia	Flavobacteriales
ESV_409	Bacteria	Proteobacteria	Alphaproteobacteria	Rhizobiales
ESV_410	Bacteria	Proteobacteria	Alphaproteobacteria	SAR11clade
ESV_411	Bacteria	Bacteroidota	Bacteroidia	unclassified
ESV_413	Bacteria	Proteobacteria	Alphaproteobacteria	Parvibaculales
ESV_416	Bacteria	Proteobacteria	Alphaproteobacteria	unclassified
ESV_421	Bacteria	Bacteroidota	Bacteroidia	Bacteroidales
ESV_423	Bacteria	Proteobacteria	Alphaproteobacteria	Rhodobacterales
ESV_424	Bacteria	Proteobacteria	Gammaproteobacteria	Pseudomonadales
ESV_426	Bacteria	Actinobacteriota	Actinobacteria	Corynebacteriales
ESV_427	Bacteria	Proteobacteria	Alphaproteobacteria	Rhodobacterales
ESV_428	Bacteria	Acidobacteriota	Vicinamibacteria	Vicinamibacterales
ESV_429	Bacteria	Proteobacteria	Gammaproteobacteria	Alteromonadales
ESV_430	Bacteria	Actinobacteriota	Acidimicrobiia	Microtrichales
ESV_432	Bacteria	Proteobacteria	Gammaproteobacteria	Oceanospirillales
ESV_433	Bacteria	Firmicutes	Negativicutes	Veillonellales-Selenomonadales
ESV_435	Bacteria	Proteobacteria	Alphaproteobacteria	Rhodospirillales
ESV_437	Bacteria	Proteobacteria	Gammaproteobacteria	Cellvibrionales
ESV_2945	Bacteria	Planctomycetota	Planctomycetes	Pirellulales
ESV_2949	Bacteria	Myxococcota	Myxococcia	Myxococcales
ESV_2961	Bacteria	Proteobacteria	Gammaproteobacteria	unclassified
ESV_2971	Bacteria	Proteobacteria	Alphaproteobacteria	Sphingomonadales
ESV_2992	Bacteria	Proteobacteria	Alphaproteobacteria	Rhodobacterales
ESV_3019	Bacteria	Bacteroidota	Bacteroidia	Cytophagales
ESV_3020	Bacteria	Proteobacteria	Alphaproteobacteria	Rhizobiales
ESV_3022	Bacteria	Verrucomicrobiota	Verrucomicrobiae	Verrucomicrobiales
ESV_3024	Bacteria	Proteobacteria	Alphaproteobacteria	Rhodobacterales
ESV_3025	Bacteria	Cyanobacteria	Cyanobacteriia	Synechococcales
ESV_3037	Bacteria	Cyanobacteria	Cyanobacteriia	Cyanobacteriales
ESV_3043	Bacteria	Planctomycetota	Planctomycetes	Pirellulales
ESV_3053	Bacteria	Cyanobacteria	Cyanobacteriia	unclassified
ESV_3055	Bacteria	Actinobacteriota	Actinobacteria	Propionibacteriales
ESV_3064	Bacteria	Proteobacteria	Alphaproteobacteria	SAR11clade
ESV_3066	Bacteria	Firmicutes	Clostridia	Clostridiales
ESV_3070	Bacteria	Proteobacteria	Gammaproteobacteria	Pseudomonadales
ESV_3071	Bacteria	Proteobacteria	Gammaproteobacteria	Alteromonadales
ESV_3077	Bacteria	Proteobacteria	Gammaproteobacteria	Alteromonadales
ESV_3086	Bacteria	Firmicutes	Clostridia	Lachnospirales
ESV_3089	Bacteria	Proteobacteria	Gammaproteobacteria	Thiotrichales
ESV_3101	Bacteria	Verrucomicrobiota	Verrucomicrobiae	Arctic97B-4 clade
ESV_3102	Bacteria	Bacteroidota	Bacteroidia	Cytophagales
ESV_3112	Bacteria	Verrucomicrobiota	Lentisphaeria	Lentisphaerales
ESV_3113	Bacteria	Cyanobacteria	Cyanobacteriia	Phormidesmiales
ESV_3123	Bacteria	Proteobacteria	Alphaproteobacteria	Parvibaculales
ESV_3138	Bacteria	Bacteroidota	Bacteroidia	Flavobacteriales
ESV_3148	Bacteria	Proteobacteria	Gammaproteobacteria	Alteromonadales
ESV_3152	Bacteria	Proteobacteria	Alphaproteobacteria	unclassified
ESV_3153	Bacteria	Proteobacteria	Alphaproteobacteria	Rhizobiales
ESV_3154	Bacteria	Proteobacteria	Alphaproteobacteria	Rhodobacterales

ESV_438	Bacteria	Actinobacteriota	Acidimicrobiia	Microtrichales
ESV_443	Bacteria	Proteobacteria	Alphaproteobacteria	unclassified
ESV_445	Bacteria	Proteobacteria	Alphaproteobacteria	Rhodobacterales
ESV_449	Bacteria	Proteobacteria	Alphaproteobacteria	unclassified
ESV_453	Bacteria	Proteobacteria	Alphaproteobacteria	Parvibaculales
ESV_455	Bacteria	Proteobacteria	Gammaproteobacteria	unclassified
ESV_457	Bacteria	Bacteroidota	Bacteroidia	Flavobacteriales
ESV_459	Bacteria	Planctomycetota	Planctomycetes	Pirellulales
ESV_460	Bacteria	Proteobacteria	Gammaproteobacteria	Vibrionales
ESV_461	Bacteria	Proteobacteria	Alphaproteobacteria	Sphingomonadales
ESV_463	Bacteria	Proteobacteria	Gammaproteobacteria	Pasteurellales
ESV_464	Bacteria	Proteobacteria	Gammaproteobacteria	unclassified
ESV_465	Bacteria	Proteobacteria	Alphaproteobacteria	Acetobacterales
ESV_466	Bacteria	Proteobacteria	Gammaproteobacteria	unclassified
ESV_467	Bacteria	Cyanobacteria	Cyanobacteriia	Synechococcales
ESV_468	Bacteria	Proteobacteria	Gammaproteobacteria	Burkholderiales
ESV_469	Bacteria	Proteobacteria	Gammaproteobacteria	Steroidobacterales
ESV_470	Bacteria	Proteobacteria	Gammaproteobacteria	Oceanospirillales
ESV_473	Bacteria	Proteobacteria	Alphaproteobacteria	Rhodobacterales
ESV_474	Bacteria	Bacteroidota	Bacteroidia	Flavobacteriales
ESV_478	Bacteria	Bacteroidota	Bacteroidia	Flavobacteriales
ESV_481	Bacteria	Proteobacteria	Gammaproteobacteria	OM182 clade
ESV_482	Bacteria	Dadabacteria	Dadabacteriia	Dadabacteriales
ESV_485	Bacteria	Proteobacteria	Alphaproteobacteria	Rhodobacterales
ESV_486	Bacteria	Cyanobacteria	Cyanobacteriia	Phormidesmiales
ESV_488	Bacteria	Cyanobacteria	Cyanobacteriia	Cyanobacteriales
ESV_491	Bacteria	Planctomycetota	Planctomycetes	Pirellulales
ESV_492	Bacteria	Cyanobacteria	Cyanobacteriia	unclassified
ESV_493	Bacteria	Proteobacteria	Gammaproteobacteria	unclassified
ESV_496	Bacteria	Proteobacteria	Alphaproteobacteria	unclassified
ESV_497	Bacteria	Proteobacteria	Gammaproteobacteria	Pasteurellales
ESV_3158	Bacteria	Bacteroidota	Bacteroidia	Cytophagales
ESV_3162	Bacteria	Proteobacteria	Alphaproteobacteria	Rhodobacterales
ESV_3185	Bacteria	Proteobacteria	Alphaproteobacteria	Rickettsiales
ESV_3199	Bacteria	Actinobacteriota	Actinobacteria	Pseudonocardiales
ESV_3204	Bacteria	Planctomycetota	Phycisphaerae	Phycisphaerales
ESV_3207	Bacteria	Proteobacteria	Alphaproteobacteria	Kordiimonadales
ESV_3210	Bacteria	Cyanobacteria	Cyanobacteriia	Cyanobacteriales
ESV_3211	Bacteria	Proteobacteria	Alphaproteobacteria	Kiloniellales
ESV_3212	Bacteria	Proteobacteria	Alphaproteobacteria	unclassified
ESV_3213	Bacteria	Proteobacteria	Alphaproteobacteria	Rhodobacterales
ESV_3228	Bacteria	Proteobacteria	Gammaproteobacteria	Nitrosococcales
ESV_3229	Bacteria	Bacteroidota	Bacteroidia	Flavobacteriales
ESV_3234	Bacteria	Bacteroidota	Bacteroidia	Flavobacteriales
ESV_3235	Bacteria	Proteobacteria	Alphaproteobacteria	Rhizobiales
ESV_3240	Bacteria	Bacteroidota	Rhodothermia	Balneolales
ESV_3246	Bacteria	Bacteroidota	Bacteroidia	Flavobacteriales
ESV_3284	Bacteria	Bacteroidota	Bacteroidia	Flavobacteriales
ESV_3287	Bacteria	Proteobacteria	Gammaproteobacteria	Tenderiales
ESV_3302	Bacteria	Proteobacteria	Alphaproteobacteria	Rhizobiales
ESV_3311	Bacteria	Deinococcota	Deinococci	Deinococcales
ESV_3316	Bacteria	Firmicutes	Clostridia	Lachnospirales
ESV_3317	Bacteria	Proteobacteria	Gammaproteobacteria	Xanthomonadales
ESV_3320	Bacteria	Verrucomicrobiota	Verrucomicrobiae	Opitutales
ESV_3327	Bacteria	Proteobacteria	Gammaproteobacteria	KI89A clade
ESV_3342	Bacteria	Planctomycetota	Planctomycetes	Pirellulales
ESV_3344	Bacteria	Proteobacteria	Gammaproteobacteria	Burkholderiales
ESV_3352	Bacteria	Bacteroidota	Bacteroidia	unclassified
ESV_3353	Bacteria	Actinobacteriota	Acidimicrobiia	Microtrichales
ESV_3357	Bacteria	Proteobacteria	Gammaproteobacteria	Alteromonadales
ESV_3358	Bacteria	Bacteroidota	Bacteroidia	Flavobacteriales
ESV_3374	Bacteria	Proteobacteria	Gammaproteobacteria	unclassified

ESV_499	Bacteria	Proteobacteria	Alphaproteobacteria	Rhizobiales
ESV_500	Bacteria	Proteobacteria	Alphaproteobacteria	Rhizobiales
ESV_501	Bacteria	Proteobacteria	Alphaproteobacteria	unclassified
ESV_505	Bacteria	Proteobacteria	Gammaproteobacteria	unclassified
ESV_507	Bacteria	Bacteroidota	Bacteroidia	Flavobacteriales
ESV_508	Bacteria	Proteobacteria	Alphaproteobacteria	Rhizobiales
ESV_509	Bacteria	Actinobacteriota	Actinobacteria	Corynebacteriales
ESV_510	Bacteria	Proteobacteria	Gammaproteobacteria	SAR86 clade
ESV_513	Bacteria	Acidobacteriota	Vicinamibacteria	Vicinamibacterales
ESV_514	Bacteria	Bacteroidota	Bacteroidia	Flavobacteriales
ESV_516	Bacteria	Cyanobacteria	Cyanobacteriia	Cyanobacteriales
ESV_518	Bacteria	Proteobacteria	Alphaproteobacteria	Rhizobiales
ESV_521	Bacteria	Proteobacteria	Gammaproteobacteria	Cellvibrionales
ESV_524	Bacteria	Firmicutes	Negativicutes	Veillonellales-Selenomonadales
ESV_526	Bacteria	Proteobacteria	Gammaproteobacteria	SAR86 clade
ESV_529	Bacteria	Proteobacteria	Alphaproteobacteria	unclassified
ESV_531	Bacteria	Firmicutes	Clostridia	Lachnospirales
ESV_532	Bacteria	Proteobacteria	Alphaproteobacteria	Kiloniellales
ESV_534	Bacteria	Proteobacteria	Alphaproteobacteria	Kordiimonadales
ESV_536	Bacteria	Planctomycetota	Planctomycetes	Pirellulales
ESV_537	Bacteria	Proteobacteria	Alphaproteobacteria	Parvibaculales
ESV_538	Bacteria	Bacteroidota	Bacteroidia	Flavobacteriales
ESV_539	Bacteria	Actinobacteriota	Actinobacteria	Corynebacteriales
ESV_540	Bacteria	Proteobacteria	Gammaproteobacteria	Oceanospirillales
ESV_541	Bacteria	Firmicutes	Clostridia	Tissierellales
ESV_542	Bacteria	Proteobacteria	Gammaproteobacteria	SAR86 clade
ESV_544	Bacteria	Proteobacteria	Alphaproteobacteria	Rhizobiales
ESV_545	Archaea	Crenarchaeota	Nitrososphaeria	Nitrosopumilales
ESV_546	Bacteria	Proteobacteria	Alphaproteobacteria	Sphingomonadales
ESV_547	Bacteria	Bacteroidota	Bacteroidia	Sphingobacteriales
ESV_548	Bacteria	Bacteroidota	Bacteroidia	Flavobacteriales

ESV_3375	Bacteria	Proteobacteria	Alphaproteobacteria	Sphingomonadales
ESV_3399	Bacteria	Bacteroidota	Bacteroidia	Flavobacteriales
ESV_3414	Bacteria	Proteobacteria	Alphaproteobacteria	SAR11clade
ESV_3428	Bacteria	Planctomycetota	Planctomycetes	Pirellulales
ESV_3429	Bacteria	Proteobacteria	Gammaproteobacteria	unclassified
ESV_3432	Bacteria	Proteobacteria	Gammaproteobacteria	Alteromonadales
ESV_3440	Bacteria	Verrucomicrobiota	Verrucomicrobiae	Opitutales
ESV_3454	Bacteria	Proteobacteria	Alphaproteobacteria	Rhodobacterales
ESV_3455	Bacteria	Bacteroidota	Bacteroidia	Flavobacteriales
ESV_3456	Bacteria	Proteobacteria	Gammaproteobacteria	Burkholderiales
ESV_3463	Bacteria	Bacteroidota	Bacteroidia	Flavobacteriales
ESV_3473	Bacteria	Proteobacteria	Gammaproteobacteria	unclassified
ESV_3493	Bacteria	Proteobacteria	Alphaproteobacteria	SAR11clade
ESV_3500	Bacteria	Proteobacteria	Gammaproteobacteria	Cellvibrionales
ESV_3508	Bacteria	Actinobacteriota	Acidimicrobiia	Microtrichales
ESV_3520	Bacteria	Proteobacteria	Gammaproteobacteria	unclassified
ESV_3551	Bacteria	Proteobacteria	Alphaproteobacteria	SAR11clade
ESV_3554	Bacteria	Bacteroidota	Bacteroidia	Flavobacteriales
ESV_3558	Bacteria	Bacteroidota	Bacteroidia	unclassified
ESV_3577	Bacteria	Verrucomicrobiota	Verrucomicrobiae	Verrucomicrobiales
ESV_3589	Bacteria	Proteobacteria	Gammaproteobacteria	unclassified
ESV_3611	Bacteria	Proteobacteria	Alphaproteobacteria	Rhodobacterales
ESV_3632	Bacteria	Proteobacteria	Alphaproteobacteria	Rhodobacterales
ESV_3639	Bacteria	Actinobacteriota	Thermoleophilia	Solirubrobacterales
ESV_3640	Bacteria	Proteobacteria	Gammaproteobacteria	Alteromonadales
ESV_3642	Bacteria	Proteobacteria	Alphaproteobacteria	Rhizobiales
ESV_3653	Bacteria	Bacteroidota	Bacteroidia	Cytophagales
ESV_3655	Bacteria	Proteobacteria	Gammaproteobacteria	Steroidobacterales
ESV_3658	Bacteria	Proteobacteria	Alphaproteobacteria	Sphingomonadales
ESV_3673	Bacteria	Proteobacteria	Alphaproteobacteria	Rhizobiales
ESV_3700	Bacteria	Cyanobacteria	Cyanobacteriia	Phormidesmiales

ESV_550	Bacteria	Verrucomicrobiota	Kiritimatiellae	Kiritimatiellales
ESV_551	Bacteria	Proteobacteria	Gammaproteobacteria	unclassified
ESV_553	Bacteria	Proteobacteria	Alphaproteobacteria	Kiloniellales
ESV_554	Bacteria	Firmicutes	Clostridia	Tissierellales
ESV_555	Bacteria	Firmicutes	Clostridia	Lachnospirales
ESV_556	Bacteria	Proteobacteria	Gammaproteobacteria	Steroidobacterales
ESV_557	Bacteria	Bacteroidota	Bacteroidia	Bacteroidales
ESV_561	Bacteria	Bacteroidota	Bacteroidia	Flavobacteriales
ESV_562	Bacteria	Bacteroidota	Bacteroidia	unclassified
ESV_565	Bacteria	Proteobacteria	Alphaproteobacteria	Rhizobiales
ESV_566	Bacteria	Verrucomicrobiota	Verrucomicrobiae	Arctic97B-4 clade
ESV_568	Bacteria	Proteobacteria	Gammaproteobacteria	Alteromonadales
ESV_570	Bacteria	Proteobacteria	Alphaproteobacteria	unclassified
ESV_572	Bacteria	Firmicutes	Clostridia	Lachnospirales
ESV_573	Bacteria	Proteobacteria	Gammaproteobacteria	unclassified
ESV_574	Bacteria	Proteobacteria	Gammaproteobacteria	Alteromonadales
ESV_575	Bacteria	Bacteroidota	Bacteroidia	Flavobacteriales
ESV_576	Bacteria	Proteobacteria	Alphaproteobacteria	SAR11clade
ESV_580	Bacteria	Bacteroidota	Bacteroidia	Cytophagales
ESV_583	Bacteria	Proteobacteria	Gammaproteobacteria	Alteromonadales
ESV_585	Bacteria	Proteobacteria	Alphaproteobacteria	Rhodobacterales
ESV_587	Bacteria	Bacteroidota	Bacteroidia	unclassified
ESV_589	Bacteria	Verrucomicrobiota	Verrucomicrobiae	Verrucomicrobiales
ESV_592	Bacteria	Firmicutes	Thermoanaerobacteria	Thermoanaerobacterales
ESV_593	Bacteria	Proteobacteria	Gammaproteobacteria	Steroidobacterales
ESV_597	Bacteria	Actinobacteriota	Actinobacteria	Corynebacteriales
ESV_598	Bacteria	Bacteroidota	Bacteroidia	Flavobacteriales
ESV_603	Bacteria	Proteobacteria	Alphaproteobacteria	Rhodobacterales
ESV_605	Bacteria	Proteobacteria	Gammaproteobacteria	Steroidobacterales
ESV_607	Bacteria	Proteobacteria	Gammaproteobacteria	Pseudomonadales
ESV_612	Bacteria	Proteobacteria	Alphaproteobacteria	unclassified

ESV_3728	Bacteria	Verrucomicrobiota	Verrucomicrobiae	Opitutales
ESV_3743	Bacteria	Actinobacteriota	Thermoleophilia	Solirubrobacterales
ESV_3744	Bacteria	Proteobacteria	Gammaproteobacteria	Cellvibrionales
ESV_3750	Bacteria	Proteobacteria	Alphaproteobacteria	Rhodospirillales
ESV_3801	Bacteria	Cyanobacteria	Cyanobacteriia	Cyanobacteriales
ESV_3808	Bacteria	Bacteroidota	Bacteroidia	Flavobacteriales
ESV_3815	Bacteria	Bacteroidota	Bacteroidia	Flavobacteriales
ESV_3819	Bacteria	Proteobacteria	Alphaproteobacteria	Defluviicoccales
ESV_3827	Bacteria	Verrucomicrobiota	Verrucomicrobiae	Verrucomicrobiales
ESV_3881	Bacteria	Firmicutes	Clostridia	Lachnospirales
ESV_3884	Bacteria	Actinobacteriota	Actinobacteria	Micrococcales
ESV_3887	Bacteria	Cyanobacteria	Cyanobacteriia	Eurycoccales
ESV_3891	Bacteria	Proteobacteria	Gammaproteobacteria	Oceanospirillales
ESV_3895	Bacteria	Proteobacteria	Alphaproteobacteria	Rhodobacterales
ESV_3921	Bacteria	Proteobacteria	Alphaproteobacteria	Rhodobacterales
ESV_3963	Bacteria	Proteobacteria	Gammaproteobacteria	Alteromonadales
ESV_3998	Bacteria	Proteobacteria	Gammaproteobacteria	Alteromonadales
ESV_4001	Bacteria	Proteobacteria	Gammaproteobacteria	Vibrionales
ESV_4026	Bacteria	Bdellovibrionota	Bdellovibrionia	Bacteriovoracales
ESV_4052	Bacteria	Proteobacteria	Alphaproteobacteria	Rhodobacterales
ESV_4055	Bacteria	Proteobacteria	Alphaproteobacteria	Caulobacterales
ESV_4066	Bacteria	Proteobacteria	Gammaproteobacteria	Oceanospirillales
ESV_4094	Bacteria	Proteobacteria	Alphaproteobacteria	Rhodobacterales
ESV_4097	Bacteria	Proteobacteria	Gammaproteobacteria	Steroidobacterales
ESV_4122	Bacteria	Bacteroidota	Bacteroidia	Flavobacteriales
ESV_4151	Bacteria	Proteobacteria	Alphaproteobacteria	unclassified
ESV_4189	Bacteria	Bacteroidota	Bacteroidia	unclassified
ESV_4198	Bacteria	Planctomycetota	Planctomycetes	Pirellulales
ESV_4237	Bacteria	Proteobacteria	Gammaproteobacteria	Nitrosococcales
ESV_4250	Bacteria	Bacteroidota	Bacteroidia	unclassified
ESV_4253	Bacteria	Proteobacteria	Alphaproteobacteria	Rhodospirillales

ESV_613	Bacteria	Proteobacteria	Gammaproteobacteria	Steroidobacterales
ESV_615	Bacteria	Proteobacteria	Alphaproteobacteria	Sphingomonadales
ESV_618	Bacteria	Bacteroidota	Bacteroidia	Flavobacteriales
ESV_622	Bacteria	Planctomycetota	Phycisphaerae	Phycisphaerales
ESV_623	Bacteria	Verrucomicrobiota	Verrucomicrobiae	Verrucomicrobiales
ESV_628	Bacteria	Proteobacteria	Alphaproteobacteria	Rickettsiales
ESV_629	Bacteria	Proteobacteria	Gammaproteobacteria	unclassified
ESV_634	Bacteria	Proteobacteria	Alphaproteobacteria	Rhodobacterales
ESV_636	Bacteria	Firmicutes	Bacilli	Lactobacillales
ESV_638	Bacteria	Actinobacteriota	Actinobacteria	Corynebacteriales
ESV_639	Bacteria	Proteobacteria	Alphaproteobacteria	Kiloniellales
ESV_641	Bacteria	Proteobacteria	Alphaproteobacteria	Rhizobiales
ESV_642	Bacteria	Proteobacteria	Alphaproteobacteria	Kiloniellales
ESV_645	Bacteria	Proteobacteria	Alphaproteobacteria	SAR11clade
ESV_647	Bacteria	Proteobacteria	Gammaproteobacteria	Cellvibrionales
ESV_649	Bacteria	Proteobacteria	Gammaproteobacteria	Pasteurellales
ESV_650	Bacteria	Proteobacteria	Gammaproteobacteria	Pseudomonadales
ESV_652	Bacteria	Bdellovibrionota	Bdellovibrionia	Bacteriovoracales
ESV_653	Bacteria	Proteobacteria	Alphaproteobacteria	Sphingomonadales
ESV_655	Bacteria	Actinobacteriota	Actinobacteria	Micrococcales
ESV_659	Bacteria	Proteobacteria	Gammaproteobacteria	KI89A clade
ESV_660	Bacteria	Proteobacteria	Gammaproteobacteria	Pasteurellales
ESV_661	Bacteria	Dadabacteria	Dadabacteriia	Dadabacteriales
ESV_662	Bacteria	Cyanobacteria	Cyanobacteriia	Cyanobacteriales
ESV_664	Bacteria	Proteobacteria	Gammaproteobacteria	Cellvibrionales
ESV_665	Bacteria	Proteobacteria	Alphaproteobacteria	Rhodobacterales
ESV_667	Bacteria	Proteobacteria	Alphaproteobacteria	Rhodobacterales
ESV_669	Bacteria	Bacteroidota	Bacteroidia	Flavobacteriales
ESV_670	Bacteria	Bacteroidota	Bacteroidia	Flavobacteriales
ESV_671	Bacteria	Firmicutes	Clostridia	Clostridiales
ESV_674	Bacteria	Firmicutes	Bacilli	Lactobacillales
ESV_4256	Bacteria	Proteobacteria	Alphaproteobacteria	Puniceispirillales
ESV_4285	Bacteria	Bacteroidota	Bacteroidia	Flavobacteriales
ESV_4286	Bacteria	Proteobacteria	Gammaproteobacteria	Steroidobacterales
ESV_4328	Bacteria	Proteobacteria	Alphaproteobacteria	Caulobacterales
ESV_4333	Bacteria	Proteobacteria	Alphaproteobacteria	Rickettsiales
ESV_4339	Bacteria	Bacteroidota	Bacteroidia	unclassified
ESV_4340	Bacteria	Acidobacteriota	Thermoanaerobaculia	Thermoanaerobaculales
ESV_4343	Bacteria	Proteobacteria	Alphaproteobacteria	Rickettsiales
ESV_4373	Bacteria	Proteobacteria	Gammaproteobacteria	unclassified
ESV_4388	Bacteria	Proteobacteria	Gammaproteobacteria	Oceanospirillales
ESV_4390	Bacteria	Proteobacteria	Alphaproteobacteria	Rhodospirillales
ESV_4419	Bacteria	Bacteroidota	Bacteroidia	Cytophagales
ESV_4450	Bacteria	Proteobacteria	Gammaproteobacteria	Pseudomonadales
ESV_4462	Bacteria	Planctomycetota	Planctomycetes	Pirellulales
ESV_4464	Bacteria	Proteobacteria	Alphaproteobacteria	Rhodobacterales
ESV_4481	Bacteria	Actinobacteriota	Acidimicrobiia	Microtrichales
ESV_4533	Bacteria	Proteobacteria	Gammaproteobacteria	Pseudomonadales
ESV_4557	Bacteria	Proteobacteria	Alphaproteobacteria	Rhizobiales
ESV_4562	Bacteria	Proteobacteria	Gammaproteobacteria	Oceanospirillales
ESV_4605	Bacteria	Cyanobacteria	Cyanobacteriia	Cyanobacteriales
ESV_4608	Bacteria	Firmicutes	Clostridia	Lachnospirales
ESV_4644	Bacteria	Bacteroidota	Bacteroidia	Flavobacteriales
ESV_4686	Bacteria	Planctomycetota	Phycisphaerae	Phycisphaerales
ESV_4687	Bacteria	Bacteroidota	Bacteroidia	Flavobacteriales
ESV_4693	Bacteria	Bacteroidota	Bacteroidia	Flavobacteriales
ESV_4734	Bacteria	Verrucomicrobiota	Lentisphaeria	Lentisphaerales
ESV_4770	Bacteria	Cyanobacteria	Cyanobacteriia	Phormidesmiales
ESV_4783	Bacteria	Proteobacteria	Gammaproteobacteria	Alteromonadales
ESV_4784	Bacteria	Proteobacteria	Gammaproteobacteria	unclassified
ESV_4790	Bacteria	Proteobacteria	Gammaproteobacteria	Burkholderiales
ESV_4845	Bacteria	Actinobacteriota	Acidimicrobiia	Microtrichales

ESV_678	Bacteria	Proteobacteria	Gammaproteobacteria	unclassified
ESV_679	Bacteria	Dadabacteria	Dadabacteriia	Dadabacteriales
ESV_682	Bacteria	Cyanobacteria	Cyanobacteriia	Phormidesmiales
ESV_686	Bacteria	Cyanobacteria	Cyanobacteriia	Synechococcales
ESV_689	Bacteria	Bacteroidota	Bacteroidia	unclassified
ESV_690	Bacteria	Proteobacteria	Gammaproteobacteria	Alteromonadales
ESV_691	Bacteria	Proteobacteria	Gammaproteobacteria	Steroidobacterales
ESV_692	Bacteria	Proteobacteria	Gammaproteobacteria	unclassified
ESV_693	Bacteria	Planctomycetota	Planctomycetes	Pirellulales
ESV_699	Bacteria	Proteobacteria	Gammaproteobacteria	unclassified
ESV_701	Bacteria	Bacteroidota	Bacteroidia	Cytophagales
ESV_706	Bacteria	Proteobacteria	Alphaproteobacteria	Kiloniellales
ESV_709	Bacteria	Planctomycetota	Planctomycetes	Pirellulales
ESV_710	Bacteria	Proteobacteria	Alphaproteobacteria	Rhizobiales
ESV_713	Bacteria	Fusobacteriota	Fusobacteriia	Fusobacteriales
ESV_715	Bacteria	Proteobacteria	Gammaproteobacteria	Steroidobacterales
ESV_719	Bacteria	Bacteroidota	Bacteroidia	Flavobacteriales
ESV_721	Bacteria	Proteobacteria	Gammaproteobacteria	SAR86 clade
ESV_727	Bacteria	Firmicutes	Clostridia	Tissierellales
ESV_728	Bacteria	Firmicutes	Clostridia	Lachnospirales
ESV_732	Bacteria	Firmicutes	Clostridia	Tissierellales
ESV_734	Bacteria	Firmicutes	Clostridia	Lachnospirales
ESV_737	Bacteria	Proteobacteria	Gammaproteobacteria	KI89A clade
ESV_744	Bacteria	Proteobacteria	Alphaproteobacteria	Parvibaculales
ESV_746	Bacteria	Proteobacteria	Gammaproteobacteria	unclassified
ESV_751	Bacteria	Bacteroidota	Bacteroidia	Flavobacteriales
ESV_759	Bacteria	Dadabacteria	Dadabacteriia	Dadabacteriales
ESV_765	Bacteria	Proteobacteria	Gammaproteobacteria	Steroidobacterales
ESV_767	Bacteria	Planctomycetota	Planctomycetes	Pirellulales
ESV_772	Bacteria	Bacteroidota	Bacteroidia	Flavobacteriales
ESV_773	Bacteria	Proteobacteria	Gammaproteobacteria	Nitrosococcales
ESV_4848	Bacteria	Acidobacteriota	Thermoanaerobaculia	Thermoanaerobaculales
ESV_4878	Bacteria	Bacteroidota	Bacteroidia	Flavobacteriales
ESV_4902	Bacteria	Bacteroidota	Bacteroidia	Flavobacteriales
ESV_4923	Bacteria	Fusobacteriota	Fusobacteriia	Fusobacteriales
ESV_4935	Bacteria	Bacteroidota	Bacteroidia	Flavobacteriales
ESV_4940	Bacteria	Proteobacteria	Gammaproteobacteria	Alteromonadales
ESV_4942	Bacteria	Chloroflexi	Dehalococcoidia	S085 clade
ESV_4948	Bacteria	Proteobacteria	Gammaproteobacteria	Granulosicoccales
ESV_4980	Bacteria	Proteobacteria	Gammaproteobacteria	unclassified
ESV_4997	Bacteria	Cyanobacteria	Cyanobacteriia	Synechococcales
ESV_5011	Bacteria	Cyanobacteria	Cyanobacteriia	Phormidesmiales
ESV_5054	Bacteria	Chloroflexi	Dehalococcoidia	SAR202 clade
ESV_5081	Bacteria	Proteobacteria	Gammaproteobacteria	Nitrosococcales
ESV_5095	Bacteria	Bacteroidota	Bacteroidia	Flavobacteriales
ESV_5116	Bacteria	Proteobacteria	Gammaproteobacteria	Oceanospirillales
ESV_5162	Bacteria	Bacteroidota	Bacteroidia	Flavobacteriales
ESV_5168	Bacteria	Bdellovibrionota	Oligoflexia	Oligoflexales
ESV_5185	Bacteria	Proteobacteria	Alphaproteobacteria	Rhodobacterales
ESV_5230	Bacteria	Proteobacteria	Gammaproteobacteria	unclassified
ESV_5243	Bacteria	Proteobacteria	Gammaproteobacteria	unclassified
ESV_5255	Bacteria	Desulfobacterota	Desulfuromonadia	unclassified
ESV_5258	Bacteria	Proteobacteria	Gammaproteobacteria	unclassified
ESV_5274	Bacteria	Verrucomicrobiota	Verrucomicrobiae	Opitutales
ESV_5293	Bacteria	Actinobacteriota	Acidimicrobiia	Microtrichales
ESV_5297	Bacteria	Bacteroidota	Bacteroidia	Bacteroidales
ESV_5298	Bacteria	Proteobacteria	Gammaproteobacteria	unclassified
ESV_5300	Bacteria	Cyanobacteria	Cyanobacteriia	Phormidesmiales
ESV_5318	Bacteria	Actinobacteriota	Acidimicrobiia	Microtrichales
ESV_5345	Bacteria	Proteobacteria	Gammaproteobacteria	Alteromonadales
ESV_5352	Bacteria	Bacteroidota	Bacteroidia	Flavobacteriales
ESV_5358	Bacteria	Proteobacteria	Gammaproteobacteria	Pasteurellales

ESV_776	Bacteria	Cyanobacteria	Cyanobacteriia	Eurycoccales
ESV_785	Bacteria	Bacteroidota	Bacteroidia	Flavobacteriales
ESV_789	Bacteria	Planctomycetota	Planctomycetes	Pirellulales
ESV_795	Bacteria	Proteobacteria	Gammaproteobacteria	unclassified
ESV_796	Bacteria	Proteobacteria	Gammaproteobacteria	unclassified
ESV_798	Bacteria	Firmicutes	Clostridia	Tissierellales
ESV_801	Archaea	Crenarchaeota	Nitrososphaeria	Nitrosopumilales
ESV_804	Bacteria	Proteobacteria	Gammaproteobacteria	Steroidobacterales
ESV_805	Bacteria	Verrucomicrobiota	Verrucomicrobiae	Opitutales
ESV_806	Bacteria	Actinobacteriota	Actinobacteria	Micrococcales
ESV_807	Bacteria	Proteobacteria	Gammaproteobacteria	Steroidobacterales
ESV_808	Archaea	Crenarchaeota	Nitrososphaeria	Nitrosopumilales
ESV_810	Bacteria	Proteobacteria	Alphaproteobacteria	Rhizobiales
ESV_811	Bacteria	Firmicutes	Clostridia	Lachnospirales
ESV_814	Bacteria	Firmicutes	Clostridia	Tissierellales
ESV_817	Bacteria	Proteobacteria	Alphaproteobacteria	Kiloniellales
ESV_818	Bacteria	Planctomycetota	Planctomycetes	Planctomycetales
ESV_823	Bacteria	Planctomycetota	Planctomycetes	Pirellulales
ESV_824	Bacteria	Cyanobacteria	Cyanobacteriia	Cyanobacteriales
ESV_825	Bacteria	Bacteroidota	Bacteroidia	Flavobacteriales
ESV_826	Bacteria	Proteobacteria	Gammaproteobacteria	Vibrionales
ESV_828	Bacteria	Proteobacteria	Alphaproteobacteria	unclassified
ESV_830	Bacteria	Proteobacteria	Gammaproteobacteria	unclassified
ESV_831	Bacteria	Proteobacteria	Alphaproteobacteria	unclassified
ESV_834	Bacteria	Proteobacteria	Gammaproteobacteria	unclassified
ESV_841	Bacteria	Bacteroidota	Bacteroidia	Cytophagales
ESV_844	Bacteria	Proteobacteria	Alphaproteobacteria	unclassified
ESV_846	Bacteria	Proteobacteria	Gammaproteobacteria	Burkholderiales
ESV_848	Bacteria	Acidobacteriota	Vicinamibacteria	unclassified
ESV_852	Bacteria	Cyanobacteria	Cyanobacteriia	Cyanobacteriales
ESV_853	Bacteria	Proteobacteria	Alphaproteobacteria	Rhodobacterales
ESV_5362	Bacteria	Proteobacteria	Gammaproteobacteria	Alteromonadales
ESV_5424	Bacteria	Bacteroidota	Bacteroidia	Chitinophagales
ESV_5478	Bacteria	Planctomycetota	Planctomycetes	Pirellulales
ESV_5490	Archaea	Crenarchaeota	Nitrososphaeria	Nitrosopumilales
ESV_5492	Bacteria	Proteobacteria	Gammaproteobacteria	unclassified
ESV_5525	Bacteria	Proteobacteria	Alphaproteobacteria	SAR11clade
ESV_5536	Bacteria	Planctomycetota	Planctomycetes	Pirellulales
ESV_5543	Bacteria	Desulfobacterota	Desulfuromonadia	unclassified
ESV_5569	Bacteria	Proteobacteria	Gammaproteobacteria	Cellvibrionales
ESV_5588	Bacteria	Verrucomicrobiota	Verrucomicrobiae	Verrucomicrobiales
ESV_5595	Bacteria	Proteobacteria	Alphaproteobacteria	SAR11clade
ESV_5715	Bacteria	Proteobacteria	Gammaproteobacteria	unclassified
ESV_5737	Bacteria	Cyanobacteria	Cyanobacteriia	Phormidesmiales
ESV_5853	Bacteria	Planctomycetota	Planctomycetes	Pirellulales
ESV_5856	Bacteria	Proteobacteria	Gammaproteobacteria	unclassified
ESV_5897	Bacteria	Proteobacteria	Gammaproteobacteria	Cellvibrionales
ESV_5912	Bacteria	Bacteroidota	Bacteroidia	Flavobacteriales
ESV_5961	Bacteria	Bacteroidota	Bacteroidia	Flavobacteriales
ESV_6007	Archaea	Crenarchaeota	Nitrososphaeria	Nitrosopumilales
ESV_6069	Bacteria	Proteobacteria	Alphaproteobacteria	Rhodospirillales
ESV_6110	Bacteria	Bacteroidota	Bacteroidia	Flavobacteriales
ESV_6177	Bacteria	Proteobacteria	Alphaproteobacteria	Rickettsiales
ESV_6269	Bacteria	Proteobacteria	Gammaproteobacteria	Vibrionales
ESV_6319	Bacteria	Bacteroidota	Bacteroidia	Flavobacteriales
ESV_6323	Bacteria	Proteobacteria	Gammaproteobacteria	Pseudomonadales
ESV_6345	Bacteria	Fusobacteriota	Fusobacteriia	Fusobacteriales
ESV_6380	Bacteria	Bacteroidota	Bacteroidia	Cytophagales
ESV_6422	Bacteria	Verrucomicrobiota	Verrucomicrobiae	Verrucomicrobiales
ESV_6493	Bacteria	Proteobacteria	Gammaproteobacteria	Alteromonadales
ESV_6604	Bacteria	Bacteroidota	Bacteroidia	Bacteroidales
ESV_6624	Bacteria	Proteobacteria	Alphaproteobacteria	Rhodobacterales

ESV_855	Archaea	Crenarchaeota	Nitrososphaeria	Nitrosopumilales
ESV_856	Bacteria	Actinobacteriota	Acidimicrobiia	Microtrichales
ESV_860	Bacteria	Proteobacteria	Gammaproteobacteria	Steroidobacterales
ESV_862	Bacteria	Proteobacteria	Gammaproteobacteria	SAR86 clade
ESV_867	Bacteria	Cyanobacteria	Cyanobacteriia	Cyanobacteriales
ESV_868	Bacteria	Proteobacteria	Alphaproteobacteria	Rhizobiales
ESV_870	Bacteria	Verrucomicrobiota	Verrucomicrobiae	Opitutales
ESV_874	Bacteria	Cyanobacteria	Cyanobacteriia	Synechococcales
ESV_878	Bacteria	Proteobacteria	Alphaproteobacteria	Rhodobacterales
ESV_880	Bacteria	Acidobacteriota	Acidobacteriae	unclassified
ESV_881	Bacteria	Proteobacteria	Alphaproteobacteria	unclassified
ESV_884	Bacteria	Proteobacteria	Gammaproteobacteria	unclassified
ESV_885	Bacteria	Proteobacteria	Alphaproteobacteria	Kiloniellales
ESV_892	Bacteria	Cyanobacteria	Cyanobacteriia	Synechococcales
ESV_902	Bacteria	Cyanobacteria	Cyanobacteriia	Cyanobacteriales
ESV_908	Bacteria	Planctomycetota	Planctomycetes	Pirellulales
ESV_909	Bacteria	Dadabacteria	Dadabacteriia	Dadabacteriales
ESV_910	Bacteria	Proteobacteria	Gammaproteobacteria	Pseudomonadales
ESV_913	Bacteria	Proteobacteria	Alphaproteobacteria	Rhizobiales
ESV_917	Bacteria	Proteobacteria	Gammaproteobacteria	unclassified
ESV_920	Bacteria	Planctomycetota	Planctomycetes	Pirellulales
ESV_922	Bacteria	Cyanobacteria	Cyanobacteriia	Eurycoccales
ESV_923	Bacteria	Proteobacteria	Gammaproteobacteria	unclassified
ESV_926	Bacteria	Proteobacteria	Gammaproteobacteria	Vibrionales
ESV_927	Bacteria	Proteobacteria	Gammaproteobacteria	Vibrionales
ESV_930	Bacteria	Proteobacteria	Gammaproteobacteria	Burkholderiales
ESV_931	Bacteria	Proteobacteria	Alphaproteobacteria	Kiloniellales
ESV_933	Bacteria	Proteobacteria	Alphaproteobacteria	Rhodobacterales
ESV_936	Bacteria	Proteobacteria	Alphaproteobacteria	Caulobacterales
ESV_938	Bacteria	Bacteroidota	Bacteroidia	Flavobacteriales
ESV_939	Bacteria	Proteobacteria	Gammaproteobacteria	Cellvibrionales

ESV_6625	Bacteria	Proteobacteria	Gammaproteobacteria	Cellvibrionales
ESV_6626	Bacteria	Proteobacteria	Alphaproteobacteria	Rhodobacterales
ESV_6635	Bacteria	Proteobacteria	Alphaproteobacteria	Rhodospirillales
ESV_6652	Bacteria	Bacteroidota	Bacteroidia	Flavobacteriales
ESV_6687	Bacteria	Bacteroidota	Rhodothermia	Balneolales
ESV_6793	Bacteria	Bdellovibrionota	Bdellovibrionia	Bacteriovoracales
ESV_6810	Bacteria	Proteobacteria	Alphaproteobacteria	Caulobacterales
ESV_6882	Bacteria	Proteobacteria	Alphaproteobacteria	Rhodospirillales
ESV_6962	Bacteria	Fusobacteriota	Fusobacteriia	Fusobacteriales
ESV_6977	Bacteria	Proteobacteria	Alphaproteobacteria	Rhodobacterales
ESV_6979	Bacteria	Bacteroidota	Bacteroidia	Flavobacteriales
ESV_6980	Archaea	Crenarchaeota	Nitrososphaeria	Nitrosopumilales
ESV_7008	Bacteria	Bacteroidota	Bacteroidia	Flavobacteriales
ESV_7012	Bacteria	Proteobacteria	Alphaproteobacteria	Rhodobacterales
ESV_7019	Bacteria	Planctomycetota	Planctomycetes	Pirellulales
ESV_7030	Bacteria	Verrucomicrobiota	Verrucomicrobiae	Opitutales
ESV_7052	Bacteria	Bacteroidota	Bacteroidia	Bacteroidales
ESV_7076	Bacteria	Proteobacteria	Alphaproteobacteria	Rhodobacterales
ESV_7132	Bacteria	Bacteroidota	Bacteroidia	Bacteroidales
ESV_7225	Bacteria	Proteobacteria	Alphaproteobacteria	Rickettsiales
ESV_7266	Bacteria	Proteobacteria	Alphaproteobacteria	Rickettsiales
ESV_7271	Bacteria	Bacteroidota	Bacteroidia	Flavobacteriales
ESV_7272	Bacteria	Proteobacteria	Gammaproteobacteria	unclassified
ESV_7328	Bacteria	Bdellovibrionota	Bdellovibrionia	Bacteriovoracales
ESV_7546	Bacteria	Bacteroidota	Bacteroidia	unclassified
ESV_7568	Bacteria	Verrucomicrobiota	Verrucomicrobiae	Opitutales
ESV_7608	Bacteria	Proteobacteria	Gammaproteobacteria	Vibrionales
ESV_7627	Bacteria	Myxococcota	Polyangia	Polyangiales
ESV_7656	Bacteria	Proteobacteria	Gammaproteobacteria	unclassified
ESV_7686	Bacteria	Bacteroidota	Bacteroidia	Flavobacteriales
ESV_7696	Bacteria	Firmicutes	Clostridia	Tissierellales

ESV_944	Bacteria	Proteobacteria	Gammaproteobacteria	Vibrionales
ESV_946	Bacteria	Bacteroidota	Bacteroidia	Flavobacteriales
ESV_952	Bacteria	Proteobacteria	Gammaproteobacteria	Steroidobacterales
ESV_954	Bacteria	Proteobacteria	Gammaproteobacteria	Burkholderiales
ESV_957	Bacteria	Bacteroidota	Bacteroidia	Cytophagales
ESV_958	Bacteria	Proteobacteria	Gammaproteobacteria	Pseudomonadales
ESV_962	Bacteria	Proteobacteria	Alphaproteobacteria	Defluviicoccales
ESV_966	Bacteria	Proteobacteria	Alphaproteobacteria	Rhodobacterales
ESV_971	Bacteria	Verrucomicrobiota	Verrucomicrobiae	Opitutales
ESV_974	Bacteria	Cyanobacteria	Cyanobacteriia	unclassified
ESV_978	Bacteria	Proteobacteria	Alphaproteobacteria	Rhodobacterales
ESV_984	Bacteria	Proteobacteria	Gammaproteobacteria	Alteromonadales
ESV_987	Bacteria	Proteobacteria	Alphaproteobacteria	Kiloniellales
ESV_989	Bacteria	Proteobacteria	Alphaproteobacteria	Kiloniellales
ESV_996	Bacteria	Proteobacteria	Alphaproteobacteria	Rhodobacterales
ESV_998	Bacteria	Planctomycetota	Planctomycetes	Pirellulales
ESV_1000	Bacteria	Cyanobacteria	Cyanobacteriia	Phormidesmiales
ESV_1001	Bacteria	Proteobacteria	Alphaproteobacteria	Rhodobacterales
ESV_1007	Bacteria	Proteobacteria	Gammaproteobacteria	Burkholderiales
ESV_1013	Bacteria	Firmicutes	Clostridia	Tissierellales
ESV_1015	Bacteria	Bacteroidota	Bacteroidia	Flavobacteriales
ESV_1019	Bacteria	Cyanobacteria	Cyanobacteriia	Synechococcales
ESV_1020	Bacteria	Proteobacteria	Gammaproteobacteria	Alteromonadales
ESV_1022	Bacteria	Proteobacteria	Gammaproteobacteria	Alteromonadales
ESV_1030	Bacteria	Cyanobacteria	Cyanobacteriia	Phormidesmiales
ESV_1033	Bacteria	Proteobacteria	Alphaproteobacteria	Kiloniellales
ESV_1037	Bacteria	Proteobacteria	Gammaproteobacteria	Alteromonadales
ESV_1040	Bacteria	Cyanobacteria	Cyanobacteriia	Cyanobacteriales
ESV_1049	Bacteria	Proteobacteria	Alphaproteobacteria	Rhodobacterales
ESV_1051	Bacteria	Proteobacteria	Gammaproteobacteria	unclassified
ESV_1052	Bacteria	Proteobacteria	Gammaproteobacteria	Cellvibrionales

ESV_7736	Bacteria	Verrucomicrobiota	Lentisphaeria	Lentisphaerales
ESV_7739	Bacteria	Proteobacteria	Alphaproteobacteria	Rhodobacterales
ESV_7762	Bacteria	Proteobacteria	Alphaproteobacteria	Rhizobiales
ESV_7776	Bacteria	Bdellovibrionota	Bdellovibrionia	Bacteriovoracales
ESV_7825	Bacteria	Bacteroidota	Bacteroidia	Flavobacteriales
ESV_7826	Bacteria	Bacteroidota	Bacteroidia	Flavobacteriales
ESV_7853	Bacteria	Planctomycetota	Planctomycetes	Pirellulales
ESV_7870	Bacteria	Proteobacteria	Gammaproteobacteria	Vibrionales
ESV_7896	Bacteria	Proteobacteria	Gammaproteobacteria	unclassified
ESV_7938	Bacteria	Proteobacteria	Alphaproteobacteria	Rhodospirillales
ESV_7976	Bacteria	Verrucomicrobiota	Verrucomicrobiae	Opitutales
ESV_7980	Bacteria	Bacteroidota	Bacteroidia	Cytophagales
ESV_7986	Bacteria	Bdellovibrionota	Oligoflexia	Oligoflexales
ESV_8102	Bacteria	Proteobacteria	Alphaproteobacteria	unclassified
ESV_8186	Bacteria	Proteobacteria	Gammaproteobacteria	unclassified
ESV_8236	Bacteria	Desulfobacterota	Desulfobacteria	Desulfobacterales
ESV_8257	Bacteria	Bacteroidota	Bacteroidia	Chitinophagales
ESV_8285	Bacteria	Patescibacteria	Gracilibacteria	unclassified
ESV_8302	Bacteria	Proteobacteria	Gammaproteobacteria	unclassified
ESV_8304	Bacteria	Verrucomicrobiota	Lentisphaeria	unclassified
ESV_8325	Bacteria	Bacteroidota	Bacteroidia	Flavobacteriales
ESV_8450	Bacteria	Bacteroidota	Bacteroidia	Bacteroidales
ESV_8451	Bacteria	Proteobacteria	Alphaproteobacteria	Rhizobiales
ESV_8504	Bacteria	Verrucomicrobiota	Lentisphaeria	Lentisphaerales
ESV_8522	Bacteria	Verrucomicrobiota	Verrucomicrobiae	Opitutales
ESV_8534	Bacteria	Verrucomicrobiota	Verrucomicrobiae	Verrucomicrobiales
ESV_8535	Bacteria	Bacteroidota	Bacteroidia	Flavobacteriales
ESV_8547	Bacteria	Bacteroidota	Bacteroidia	Bacteroidales
ESV_8557	Bacteria	Proteobacteria	Gammaproteobacteria	Cellvibrionales
ESV_8561	Bacteria	Planctomycetota	Planctomycetes	Pirellulales
ESV_8578	Bacteria	Proteobacteria	Alphaproteobacteria	Rhodobacterales

ESV_1057	Bacteria	Cyanobacteria	Cyanobacteriia	Cyanobacteriales
ESV_1063	Bacteria	Planctomycetota	Planctomycetes	Pirellulales
ESV_1068	Bacteria	Verrucomicrobiota	Lentisphaeria	Lentisphaerales
ESV_1069	Bacteria	Proteobacteria	Gammaproteobacteria	Pseudomonadales
ESV_1073	Bacteria	Firmicutes	Clostridia	Tissierellales
ESV_1077	Bacteria	Dadabacteria	Dadabacteriia	Dadabacteriales
ESV_1078	Bacteria	Acidobacteriota	Vicinamibacteria	Vicinamibacterales
ESV_1081	Bacteria	Proteobacteria	Gammaproteobacteria	Steroidobacterales
ESV_1091	Bacteria	Cyanobacteria	Cyanobacteriia	Synechococcales
ESV_1092	Bacteria	Proteobacteria	Gammaproteobacteria	unclassified
ESV_1094	Bacteria	Firmicutes	Clostridia	Tissierellales
ESV_1095	Bacteria	Planctomycetota	Phycisphaerae	Phycisphaerales
ESV_1097	Bacteria	Planctomycetota	Planctomycetes	Pirellulales
ESV_1098	Bacteria	Cyanobacteria	Cyanobacteriia	Cyanobacteriales
ESV_1099	Bacteria	Cyanobacteria	Cyanobacteriia	Eurycoccales
ESV_1100	Bacteria	Proteobacteria	Gammaproteobacteria	Pseudomonadales
ESV_1106	Bacteria	Cyanobacteria	Cyanobacteriia	Cyanobacteriales
ESV_1112	Bacteria	Proteobacteria	Alphaproteobacteria	Rickettsiales
ESV_1116	Bacteria	Bacteroidota	Bacteroidia	Flavobacteriales
ESV_1117	Bacteria	Patescibacteria	Gracilibacteria	unclassified
ESV_1119	Bacteria	Acidobacteriota	Thermoanaerobaculia	Thermoanaerobaculales
ESV_1120	Bacteria	Cyanobacteria	Cyanobacteriia	Cyanobacteriales
ESV_1121	Bacteria	Proteobacteria	Alphaproteobacteria	Rhodobacterales
ESV_1122	Bacteria	Bacteroidota	Bacteroidia	unclassified
ESV_1124	Bacteria	Proteobacteria	Gammaproteobacteria	Cellvibrionales
ESV_1126	Bacteria	Proteobacteria	Gammaproteobacteria	Vibrionales
ESV_1128	Bacteria	Proteobacteria	Gammaproteobacteria	unclassified
ESV_1133	Bacteria	Cyanobacteria	Cyanobacteriia	Cyanobacteriales
ESV_1135	Bacteria	Proteobacteria	Gammaproteobacteria	unclassified
ESV_1140	Bacteria	Proteobacteria	Alphaproteobacteria	unclassified
ESV_1146	Bacteria	Bdellovibrionota	Oligoflexia	Oligoflexales
ESV_8582	Bacteria	Bdellovibrionota	Bdellovibrionia	Bacteriovoracales
ESV_8629	Bacteria	Proteobacteria	Alphaproteobacteria	unclassified
ESV_8650	Bacteria	Proteobacteria	Gammaproteobacteria	Oceanospirillales
ESV_8653	Bacteria	Fusobacteriota	Fusobacteriia	Fusobacteriales
ESV_8658	Bacteria	Proteobacteria	Gammaproteobacteria	Cellvibrionales
ESV_8690	Bacteria	Bacteroidota	Bacteroidia	Flavobacteriales
ESV_8833	Bacteria	Verrucomicrobiota	Verrucomicrobiae	Opitutales
ESV_8866	Bacteria	Verrucomicrobiota	Verrucomicrobiae	Verrucomicrobiales
ESV_8958	Bacteria	Bdellovibrionota	Bdellovibrionia	Bacteriovoracales
ESV_8964	Bacteria	Bacteroidota	Bacteroidia	unclassified
ESV_9013	Bacteria	Bacteroidota	Bacteroidia	Flavobacteriales
ESV_9062	Bacteria	Proteobacteria	Gammaproteobacteria	Alteromonadales
ESV_9071	Bacteria	Patescibacteria	Gracilibacteria	unclassified
ESV_9072	Bacteria	Bacteroidota	Bacteroidia	unclassified
ESV_9077	Bacteria	Bacteroidota	Bacteroidia	Flavobacteriales
ESV_9105	Bacteria	Bacteroidota	Bacteroidia	Flavobacteriales
ESV_9119	Bacteria	Verrucomicrobiota	Verrucomicrobiae	Verrucomicrobiales
ESV_9177	Bacteria	Bacteroidota	Bacteroidia	unclassified
ESV_9179	Bacteria	Proteobacteria	Gammaproteobacteria	unclassified
ESV_9184	Bacteria	Bacteroidota	Bacteroidia	Bacteroidales
ESV_9229	Bacteria	Proteobacteria	Gammaproteobacteria	Cellvibrionales
ESV_9248	Bacteria	Verrucomicrobiota	Kiritimatiellae	Kiritimatiellales
ESV_9250	Bacteria	Proteobacteria	Gammaproteobacteria	Alteromonadales
ESV_9254	Bacteria	Proteobacteria	Alphaproteobacteria	SAR11clade
ESV_9271	Bacteria	Proteobacteria	Gammaproteobacteria	Vibrionales
ESV_9371	Bacteria	Bacteroidota	Bacteroidia	Chitinophagales
ESV_9408	Bacteria	Proteobacteria	Alphaproteobacteria	SAR11clade
ESV_9410	Bacteria	Bacteroidota	Bacteroidia	unclassified
ESV_9428	Bacteria	Proteobacteria	Gammaproteobacteria	unclassified
ESV_9484	Bacteria	Proteobacteria	Alphaproteobacteria	unclassified
ESV_9497	Bacteria	Proteobacteria	Gammaproteobacteria	unclassified

ESV_1148	Bacteria	Proteobacteria	Gammaproteobacteria	unclassified
ESV_1151	Bacteria	Proteobacteria	Alphaproteobacteria	unclassified
ESV_1154	Bacteria	Cyanobacteria	Cyanobacteriia	Cyanobacteriales
ESV_1157	Bacteria	Proteobacteria	Alphaproteobacteria	Rhizobiales
ESV_1158	Bacteria	Proteobacteria	Gammaproteobacteria	Steroidobacterales
ESV_1162	Bacteria	Bacteroidota	Bacteroidia	unclassified
ESV_1169	Bacteria	Cyanobacteria	Cyanobacteriia	Cyanobacteriales
ESV_1183	Bacteria	Cyanobacteria	Cyanobacteriia	Cyanobacteriales
ESV_1184	Bacteria	Planctomycetota	Planctomycetes	Pirellulales
ESV_1185	Bacteria	Desulfobacterota	Desulfovibrionia	Desulfovibrionales
ESV_1189	Bacteria	Proteobacteria	Alphaproteobacteria	Parvibaculales
ESV_1190	Bacteria	Firmicutes	Clostridia	Tissierellales
ESV_1200	Archaea	Thermoplasmatota	Thermoplasmata	unclassified
ESV_1202	Bacteria	Verrucomicrobiota	Lentisphaeria	Lentisphaerales
ESV_1206	Bacteria	Proteobacteria	Alphaproteobacteria	Kiloniellales
ESV_1211	Bacteria	Acidobacteriota	Thermoanaerobaculia	Thermoanaerobaculales
ESV_1212	Bacteria	Bacteroidota	Bacteroidia	Flavobacteriales
ESV_1215	Bacteria	Proteobacteria	Gammaproteobacteria	unclassified
ESV_1218	Bacteria	Cyanobacteria	Cyanobacteriia	Cyanobacteriales
ESV_1223	Bacteria	Proteobacteria	Gammaproteobacteria	Alteromonadales
ESV_1224	Bacteria	Proteobacteria	Gammaproteobacteria	Oceanospirillales
ESV_1230	Bacteria	Proteobacteria	Gammaproteobacteria	unclassified
ESV_1239	Bacteria	Proteobacteria	Alphaproteobacteria	unclassified
ESV_1240	Bacteria	Proteobacteria	Gammaproteobacteria	unclassified
ESV_1248	Bacteria	Proteobacteria	Alphaproteobacteria	unclassified
ESV_1249	Bacteria	Proteobacteria	Gammaproteobacteria	unclassified
ESV_1251	Bacteria	Proteobacteria	Gammaproteobacteria	SAR86 clade
ESV_1258	Bacteria	Proteobacteria	Alphaproteobacteria	SAR11clade
ESV_1259	Bacteria	Proteobacteria	Alphaproteobacteria	Rhizobiales
ESV_1261	Bacteria	Proteobacteria	Gammaproteobacteria	Oceanospirillales
ESV_1262	Bacteria	Proteobacteria	Alphaproteobacteria	Rickettsiales
ESV_9551	Bacteria	Proteobacteria	Alphaproteobacteria	Rhodobacterales
ESV_9571	Bacteria	Bacteroidota	Bacteroidia	Flavobacteriales
ESV_9609	Bacteria	Proteobacteria	Gammaproteobacteria	Oceanospirillales
ESV_9640	Bacteria	Proteobacteria	Gammaproteobacteria	Cellvibrionales
ESV_9657	Bacteria	Proteobacteria	Alphaproteobacteria	Rhodobacterales
ESV_9679	Bacteria	Proteobacteria	Alphaproteobacteria	unclassified
ESV_9694	Bacteria	Proteobacteria	Gammaproteobacteria	unclassified
ESV_9700	Bacteria	Bdellovibrionota	Bdellovibrionia	Bacteriovoracales
ESV_9719	Bacteria	Bacteroidota	Bacteroidia	Flavobacteriales
ESV_9747	Bacteria	Bacteroidota	Bacteroidia	Flavobacteriales
ESV_9781	Bacteria	Bacteroidota	Bacteroidia	Flavobacteriales
ESV_9868	Bacteria	Proteobacteria	Gammaproteobacteria	unclassified
ESV_9895	Bacteria	Proteobacteria	Gammaproteobacteria	Oceanospirillales
ESV_9913	Bacteria	Verrucomicrobiota	Omnitrophia	Omnitrophales
ESV_9950	Bacteria	Bacteroidota	Bacteroidia	Flavobacteriales
ESV_10006	Bacteria	Cyanobacteria	Cyanobacteriia	Phormidesmiales
ESV_10042	Bacteria	Proteobacteria	Gammaproteobacteria	Tenderiales
ESV_10052	Bacteria	Bacteroidota	Bacteroidia	Flavobacteriales
ESV_10117	Bacteria	Proteobacteria	Gammaproteobacteria	unclassified
ESV_10153	Bacteria	Desulfobacterota	Desulfobacteria	Desulfobacterales
ESV_10158	Bacteria	Bdellovibrionota	Bdellovibrionia	Bacteriovoracales
ESV_10189	Bacteria	Bdellovibrionota	Bdellovibrionia	Bacteriovoracales
ESV_10197	Bacteria	Bacteroidota	Bacteroidia	Flavobacteriales
ESV_10236	Bacteria	Bacteroidota	Bacteroidia	unclassified
ESV_10244	Bacteria	Bdellovibrionota	Bdellovibrionia	Bacteriovoracales
ESV_10258	Bacteria	Proteobacteria	Gammaproteobacteria	Alteromonadales
ESV_10262	Bacteria	Bacteroidota	Bacteroidia	Flavobacteriales
ESV_10379	Bacteria	Proteobacteria	Gammaproteobacteria	Thiotrichales
ESV_10435	Bacteria	Bacteroidota	Bacteroidia	Chitinophagales
ESV_10436	Bacteria	Bdellovibrionota	Oligoflexia	Oligoflexales
ESV_10463	Bacteria	Proteobacteria	Gammaproteobacteria	Thiomicrospirales

ESV_1263	Bacteria	Proteobacteria	Gammaproteobacteria	unclassified
ESV_1264	Bacteria	Acidobacteriota	Vicinamibacteria	Vicinamibacterales
ESV_1266	Bacteria	Cyanobacteria	Cyanobacteriia	Cyanobacteriales
ESV_1267	Bacteria	Verrucomicrobiota	Verrucomicrobiae	Verrucomicrobiales
ESV_1268	Bacteria	Proteobacteria	Gammaproteobacteria	Nitrosococcales
ESV_1269	Bacteria	Proteobacteria	Alphaproteobacteria	Rhodobacterales
ESV_1274	Bacteria	Planctomycetota	Planctomycetes	Pirellulales
ESV_1276	Bacteria	Proteobacteria	Alphaproteobacteria	SAR11clade
ESV_1278	Bacteria	Proteobacteria	Gammaproteobacteria	Alteromonadales
ESV_1281	Bacteria	Bacteroidota	Bacteroidia	Cytophagales
ESV_1282	Bacteria	Proteobacteria	Alphaproteobacteria	Puniceispirillales
ESV_1283	Archaea	Thermoplasmatota	Thermoplasmata	unclassified
ESV_1289	Bacteria	Proteobacteria	Alphaproteobacteria	Parvibaculales
ESV_1290	Bacteria	Planctomycetota	Phycisphaerae	Phycisphaerales
ESV_1291	Bacteria	Firmicutes	Clostridia	Clostridiales
ESV_1298	Bacteria	Bacteroidota	Bacteroidia	Flavobacteriales
ESV_1299	Bacteria	Proteobacteria	Gammaproteobacteria	unclassified
ESV_1301	Bacteria	Cyanobacteria	Cyanobacteriia	Cyanobacteriales
ESV_1304	Bacteria	Planctomycetota	Planctomycetes	Pirellulales
ESV_1307	Bacteria	Planctomycetota	Planctomycetes	Pirellulales
ESV_1310	Bacteria	Cyanobacteria	Cyanobacteriia	Cyanobacteriales
ESV_1317	Bacteria	Proteobacteria	Gammaproteobacteria	Burkholderiales
ESV_1320	Bacteria	Proteobacteria	Gammaproteobacteria	Cellvibrionales
ESV_1324	Bacteria	Fusobacteriota	Fusobacteriia	Fusobacteriales
ESV_1326	Bacteria	Proteobacteria	Gammaproteobacteria	Cellvibrionales
ESV_1327	Bacteria	Proteobacteria	Gammaproteobacteria	Cellvibrionales
ESV_1332	Bacteria	Cyanobacteria	Cyanobacteriia	Cyanobacteriales
ESV_1334	Bacteria	Proteobacteria	Gammaproteobacteria	unclassified
ESV_1336	Bacteria	Proteobacteria	Alphaproteobacteria	Rhodobacterales
ESV_1340	Bacteria	Proteobacteria	Gammaproteobacteria	Vibrionales
ESV_1344	Bacteria	Proteobacteria	Gammaproteobacteria	SAR86 clade
ESV_10465	Bacteria	Proteobacteria	Gammaproteobacteria	Oceanospirillales
ESV_10466	Bacteria	Verrucomicrobiota	Omnitrophia	Omnitrophales
ESV_10515	Bacteria	Bacteroidota	Bacteroidia	Flavobacteriales
ESV_10517	Bacteria	Planctomycetota	Phycisphaerae	Phycisphaerales
ESV_10523	Bacteria	Proteobacteria	Gammaproteobacteria	Vibrionales
ESV_10560	Bacteria	Planctomycetota	Phycisphaerae	Phycisphaerales
ESV_10567	Bacteria	Bacteroidota	Bacteroidia	Flavobacteriales
ESV_10570	Bacteria	Proteobacteria	Gammaproteobacteria	Coxiellales
ESV_10646	Bacteria	Bdellovibrionota	Bdellovibrionia	Bacteriovoracales
ESV_10692	Bacteria	Bdellovibrionota	Bdellovibrionia	Bacteriovoracales
ESV_10731	Bacteria	Verrucomicrobiota	Verrucomicrobiae	Verrucomicrobiales
ESV_10739	Bacteria	Patescibacteria	Gracilibacteria	unclassified
ESV_10781	Bacteria	Bacteroidota	Bacteroidia	Cytophagales
ESV_10782	Bacteria	Bacteroidota	Bacteroidia	Flavobacteriales
ESV_10783	Bacteria	Bacteroidota	Bacteroidia	Flavobacteriales
ESV_10836	Bacteria	Cyanobacteria	Cyanobacteriia	Cyanobacteriales
ESV_10839	Bacteria	Proteobacteria	Alphaproteobacteria	Rhodobacterales
ESV_10879	Bacteria	Bacteroidota	Bacteroidia	Flavobacteriales
ESV_10898	Bacteria	Bacteroidota	Bacteroidia	Cytophagales
ESV_10899	Bacteria	Bacteroidota	Bacteroidia	Cytophagales
ESV_10906	Bacteria	Bdellovibrionota	Bdellovibrionia	Bacteriovoracales
ESV_10934	Bacteria	Bacteroidota	Bacteroidia	Bacteroidales
ESV_10950	Bacteria	Bacteroidota	Bacteroidia	Flavobacteriales
ESV_10952	Bacteria	Verrucomicrobiota	Kiritimatiellae	Kiritimatiellales
ESV_10953	Bacteria	Proteobacteria	Gammaproteobacteria	Alteromonadales
ESV_10976	Bacteria	Proteobacteria	Alphaproteobacteria	Rickettsiales
ESV_11046	Bacteria	Proteobacteria	Alphaproteobacteria	Rhizobiales
ESV_11075	Bacteria	Patescibacteria	Gracilibacteria	unclassified
ESV_11088	Bacteria	Planctomycetota	Planctomycetes	Pirellulales
ESV_11089	Bacteria	Proteobacteria	Alphaproteobacteria	Caulobacterales
ESV_11126	Bacteria	Proteobacteria	Alphaproteobacteria	Rhodospirillales

ESV_1352	Bacteria	Proteobacteria	Gammaproteobacteria	Alteromonadales
ESV_1356	Bacteria	Myxococcota	Polyangia	Haliangiales
ESV_1360	Bacteria	Proteobacteria	Gammaproteobacteria	Oceanospirillales
ESV_1368	Bacteria	Proteobacteria	Gammaproteobacteria	Cellvibrionales
ESV_1377	Bacteria	Actinobacteriota	Acidimicrobiia	Microtrichales
ESV_1385	Bacteria	Planctomycetota	Planctomycetes	Pirellulales
ESV_1399	Bacteria	Planctomycetota	Planctomycetes	Pirellulales
ESV_1402	Archaea	Crenarchaeota	Nitrososphaeria	Nitrosopumilales
ESV_1409	Bacteria	Proteobacteria	Alphaproteobacteria	Parvibaculales
ESV_1414	Bacteria	Bacteroidota	Bacteroidia	Flavobacteriales
ESV_1416	Bacteria	Acidobacteriota	Vicinamibacteria	unclassified
ESV_1419	Bacteria	Proteobacteria	Gammaproteobacteria	Vibrionales
ESV_1424	Bacteria	Proteobacteria	Gammaproteobacteria	Oceanospirillales
ESV_1425	Bacteria	Bacteroidota	Bacteroidia	Flavobacteriales
ESV_1431	Bacteria	Proteobacteria	Alphaproteobacteria	Rhizobiales
ESV_1433	Bacteria	Acidobacteriota	Vicinamibacteria	unclassified
ESV_1435	Bacteria	Deinococcota	Deinococci	Thermales
ESV_1436	Bacteria	Proteobacteria	Alphaproteobacteria	Sphingomonadales
ESV_1439	Bacteria	Proteobacteria	Alphaproteobacteria	unclassified
ESV_1440	Bacteria	Chloroflexi	Dehalococcoidia	SAR202 clade
ESV_1441	Bacteria	Bacteroidota	Bacteroidia	Flavobacteriales
ESV_1457	Bacteria	Proteobacteria	Gammaproteobacteria	Alteromonadales
ESV_1458	Bacteria	Bacteroidota	Bacteroidia	unclassified
ESV_1460	Bacteria	Proteobacteria	Gammaproteobacteria	Steroidobacterales
ESV_1461	Archaea	Crenarchaeota	Nitrososphaeria	Nitrosopumilales
ESV_1469	Bacteria	Proteobacteria	Alphaproteobacteria	SAR11clade
ESV_1484	Bacteria	Proteobacteria	Alphaproteobacteria	unclassified
ESV_1487	Bacteria	Proteobacteria	Alphaproteobacteria	Rhodobacterales
ESV_1492	Bacteria	Proteobacteria	Alphaproteobacteria	unclassified
ESV_1493	Bacteria	Bacteroidota	Bacteroidia	Flavobacteriales
ESV_1494	Bacteria	Cyanobacteria	Cyanobacteriia	Phormidesmiales
ESV_11131	Bacteria	Acidobacteriota	Thermoanaerobaculia	Thermoanaerobaculales
ESV_11134	Bacteria	Bdellovibrionota	Bdellovibrionia	Bdellovibrionales
ESV_11249	Bacteria	Proteobacteria	Gammaproteobacteria	Alteromonadales
ESV_11250	Bacteria	Campilobacterota	Campylobacteria	Campylobacterales
ESV_11347	Bacteria	Bacteroidota	Bacteroidia	Flavobacteriales
ESV_11369	Bacteria	Bacteroidota	Bacteroidia	unclassified
ESV_11374	Bacteria	Verrucomicrobiota	Verrucomicrobiae	Opitutales
ESV_11501	Bacteria	Proteobacteria	Gammaproteobacteria	unclassified
ESV_11526	Bacteria	Bdellovibrionota	Bdellovibrionia	Bacteriovoracales
ESV_11555	Bacteria	Bacteroidota	Bacteroidia	Chitinophagales
ESV_11603	Bacteria	Desulfobacterota	Desulfobacteria	Desulfobacterales
ESV_11644	Bacteria	Bdellovibrionota	Bdellovibrionia	Bacteriovoracales
ESV_11671	Bacteria	Proteobacteria	Alphaproteobacteria	Rhodobacterales
ESV_11673	Bacteria	Proteobacteria	Alphaproteobacteria	Kordiimonadales
ESV_11676	Bacteria	Verrucomicrobiota	Verrucomicrobiae	Opitutales
ESV_11705	Bacteria	Proteobacteria	Gammaproteobacteria	Oceanospirillales
ESV_11730	Bacteria	Bacteroidota	Bacteroidia	Bacteroidales
ESV_11732	Bacteria	Firmicutes	Clostridia	unclassified
ESV_11799	Bacteria	Proteobacteria	Gammaproteobacteria	unclassified
ESV_11822	Bacteria	Proteobacteria	Alphaproteobacteria	unclassified
ESV_11854	Bacteria	Bacteroidota	Bacteroidia	Bacteroidales
ESV_11910	Bacteria	Proteobacteria	Gammaproteobacteria	Oceanospirillales
ESV_11965	Bacteria	Proteobacteria	Gammaproteobacteria	unclassified
ESV_11966	Bacteria	Proteobacteria	Gammaproteobacteria	Cellvibrionales
ESV_11995	Bacteria	Proteobacteria	Gammaproteobacteria	Burkholderiales
ESV_12094	Bacteria	Bacteroidota	Bacteroidia	unclassified
ESV_12098	Bacteria	Bdellovibrionota	Bdellovibrionia	Bacteriovoracales
ESV_12224	Bacteria	Proteobacteria	Alphaproteobacteria	unclassified
ESV_12278	Bacteria	Bdellovibrionota	Bdellovibrionia	Bdellovibrionales
ESV_12280	Bacteria	Planctomycetota	Phycisphaerae	unclassified
ESV_12353	Bacteria	Proteobacteria	Gammaproteobacteria	unclassified

ESV_1498	Bacteria	Proteobacteria	Gammaproteobacteria	Enterobacterales
ESV_1499	Bacteria	Planctomycetota	Planctomycetes	Planctomycetales
ESV_1513	Bacteria	Proteobacteria	Alphaproteobacteria	unclassified
ESV_1514	Bacteria	Cyanobacteria	Cyanobacteriia	Synechococcales
ESV_1515	Bacteria	Bacteroidota	Bacteroidia	Flavobacteriales
ESV_1523	Bacteria	Firmicutes	Clostridia	Lachnospirales
ESV_1524	Bacteria	Proteobacteria	Alphaproteobacteria	unclassified
ESV_1535	Bacteria	Proteobacteria	Alphaproteobacteria	Parvibaculales
ESV_1537	Bacteria	Actinobacteriota	Acidimicrobiia	Microtrichales
ESV_1542	Bacteria	Bdellovibrionota	Bdellovibrionia	Bacteriovoracales
ESV_1543	Bacteria	Verrucomicrobiota	Lentisphaeria	Lentisphaerales
ESV_1549	Bacteria	Planctomycetota	Planctomycetes	Pirellulales
ESV_1551	Bacteria	Planctomycetota	Phycisphaerae	Tepidisphaerales
ESV_1557	Bacteria	Proteobacteria	Alphaproteobacteria	Rhodobacterales
ESV_1558	Bacteria	Proteobacteria	Gammaproteobacteria	Vibrionales
ESV_1559	Bacteria	Proteobacteria	Alphaproteobacteria	Rhizobiales
ESV_1560	Bacteria	Proteobacteria	Gammaproteobacteria	Vibrionales
ESV_1563	Bacteria	Bacteroidota	Bacteroidia	Flavobacteriales
ESV_1565	Bacteria	Cyanobacteria	Cyanobacteriia	unclassified
ESV_1568	Bacteria	Planctomycetota	Planctomycetes	Pirellulales
ESV_1569	Bacteria	Verrucomicrobiota	Verrucomicrobiae	Opitutales
ESV_1581	Bacteria	Cyanobacteria	Cyanobacteriia	unclassified
ESV_1584	Bacteria	Firmicutes	Clostridia	Lachnospirales
ESV_1586	Bacteria	Proteobacteria	Alphaproteobacteria	Rhodobacterales
ESV_1587	Bacteria	Cyanobacteria	Cyanobacteriia	Cyanobacteriales
ESV_1588	Bacteria	Proteobacteria	Alphaproteobacteria	Rhodobacterales
ESV_1591	Bacteria	Planctomycetota	Planctomycetes	Pirellulales
ESV_1595	Bacteria	Proteobacteria	Alphaproteobacteria	Thalassobaculales
ESV_1596	Bacteria	Planctomycetota	Planctomycetes	Pirellulales
ESV_1597	Bacteria	Actinobacteriota	Acidimicrobiia	Microtrichales
ESV_12354	Bacteria	Bdellovibrionota	Bdellovibrionia	Bacteriovoracales
ESV_12372	Bacteria	Verrucomicrobiota	Kiritimatiellae	Kiritimatiellales
ESV_12471	Bacteria	Verrucomicrobiota	Verrucomicrobiae	Verrucomicrobiales
ESV_12472	Bacteria	Proteobacteria	Gammaproteobacteria	Alteromonadales
ESV_12474	Bacteria	Bacteroidota	Bacteroidia	Flavobacteriales
ESV_12477	Bacteria	Proteobacteria	Gammaproteobacteria	Cellvibrionales
ESV_12478	Bacteria	Proteobacteria	Alphaproteobacteria	unclassified
ESV_12559	Bacteria	Proteobacteria	Gammaproteobacteria	unclassified
ESV_12627	Bacteria	Verrucomicrobiota	Kiritimatiellae	Kiritimatiellales
ESV_12754	Bacteria	Proteobacteria	Alphaproteobacteria	Caulobacterales
ESV_12775	Bacteria	Bdellovibrionota	Bdellovibrionia	Bacteriovoracales
ESV_12780	Bacteria	Bdellovibrionota	Bdellovibrionia	Bacteriovoracales
ESV_12850	Bacteria	Proteobacteria	Gammaproteobacteria	unclassified
ESV_12930	Bacteria	Verrucomicrobiota	Omnitrophia	Omnitrophales
ESV_12931	Bacteria	Bdellovibrionota	Bdellovibrionia	Bacteriovoracales
ESV_12934	Bacteria	Bacteroidota	Bacteroidia	unclassified
ESV_13290	Bacteria	Bdellovibrionota	Bdellovibrionia	Bacteriovoracales
ESV_13298	Bacteria	Proteobacteria	Alphaproteobacteria	unclassified
ESV_13610	Bacteria	Proteobacteria	Gammaproteobacteria	Cellvibrionales
ESV_13614	Bacteria	Campilobacterota	Campylobacteria	Campylobacterales
ESV_13687	Bacteria	Planctomycetota	Planctomycetes	Pirellulales
ESV_14463	Bacteria	Bacteroidota	Bacteroidia	Sphingobacteriales
ESV_15251	Bacteria	Proteobacteria	Alphaproteobacteria	unclassified
ESV_16202	Bacteria	Bacteroidota	Bacteroidia	Flavobacteriales
ESV_16616	Bacteria	Proteobacteria	Gammaproteobacteria	Alteromonadales
ESV_18091	Bacteria	Proteobacteria	Gammaproteobacteria	unclassified
ESV_18280	Bacteria	Proteobacteria	Gammaproteobacteria	unclassified
ESV_18500	Bacteria	Bacteroidota	Bacteroidia	Bacteroidales
ESV_20204	Bacteria	Spirochaetota	Spirochaetia	Spirochaetales

ANNEX 4. RRPP analysis

Pairwise Randomization of Residuals in a Permutation Procedure (RRPP) for the prokaryotic communities within **A.** sample type (seawater, substrate and each of the 6 species of LBFs) and, **B.** area of the reef (reef flat, reef slope at 10 and 20 m depth). This test was conducted on both the Bray-Curtis and Jaccard dissimilarity matrix using SS typeI.

A. Pairwise comparisons between sample types. Significance codes: 0.05*

	p - value
seawater vs substrate	0.001*
SEAWATER VS LBFs	
seawater vs *H. depressa*	0.001*
seawater vs *A. lessonii*	0.001*
seawater vs *A. lobifera*	0.001*
seawater vs *A. radiata*	0.001*
seawater vs *C. spengleri*	0.001*
seawater vs *N. calcar*	0.001*
SUBSTRATE vs LBFs	
substrate vs *H. depressa*	0.001*
substrate vs *A. lessonii*	0.001*
substrate vs *A. lobifera*	0.017*
substrate vs *A. radiata*	0.001*
substrate vs *C. spengleri*	0.001*
substrate vs *N. calcar*	0.001*

	p - value
LBFs vs LBFs	
H. depressa vs A. lessonii	0.001*
H. depressa vs A. lobifera	0.003*
H. depressa vs A. radiata	0.008*
H. depressa vs C. spengleri	0.001*
H. depressa vs N. calcar	0.003*
A. lessonii vs A. lobifera	0.272
A. lessonii vs A. radiata	0.002*
A. lessonii vs C. spengleri	0.015*
A. lessonii vs N. calcar	0.152
A. lobifera vs A. radiata	0.060
A. lobifera vs C. spengleri	0.124
A. lobifera vs N. calcar	0.024*
A. radiata vs C. spengleri	0.003*
A. radiata vs N. calcar	0.276
C. spengleri vs N. calcar	0.136

B. Pairwise comparisons for each island. Significance codes: 0.05*

	Badi		**Padjenekang**	
	R^2 (%)	**p-value**	**R^2 (%)**	**p-value**
Sample type	31.18	0.001*	31.04	0.001*
Area	3.95	0.001*	4.65	0.001*
Sample type:area	9.44	0.010*	8.13	0.115

C. Pairwise comparisons between sample types in each island. Significance codes: 0.05*

	Badi	Padjenekang
	p - value	p - value
seawater vs substrate	0.001*	0.001*
SEAWATER VS LBFs		
seawater vs *H. depressa*	0.001*	0.001*
seawater vs *A. lessonii*	0.001*	0.001*
seawater vs *A. lobifera*	0.001*	0.001*
seawater vs *A. radiata*	0.001*	0.001*
seawater vs *C. spengleri*	0.001*	0.001*
seawater vs *N. calcar*	0.001*	0.001*
SUBSTRATE vs LBFs		
substrate vs *H. depressa*	0.004*	0.005*
substrate vs *A. lessonii*	0.086	0.004*
substrate vs *A. lobifera*	0.477	0.014*
substrate vs *A. radiata*	0.014*	0.001*
substrate vs *C. spengleri*	0.012*	0.001*
substrate vs *N. calcar*	0.015*	0.016*

	Badi	Padjenekang
	p - value	p - value
LBFs vs LBFs		
H. depressa vs A. lessonii	0.001*	0.001*
H. depressa vs A. lobifera	0.013*	0.032*
H. depressa vs A. radiata	0.381	0.013*
H. depressa vs C. spengleri	0.001*	0.002*
H. depressa vs N. calcar	0.015*	0.501
A. lessonii vs A. lobifera	0.421	0.272
A. lessonii vs A. radiata	0.024*	0.030*
A. lessonii vs C. spengleri	0.019*	0.117
A. lessonii vs N. calcar	0.186	0.118
A. lobifera vs A. radiata	0.194	0.195
A. lobifera vs C. spengleri	0.111	0.344
A. lobifera vs N. calcar	0.029*	0.089
A. radiata vs C. spengleri	0.003*	0.073
A. radiata vs N. calcar	0.097	0.412
C. spengleri vs N. calcar	0.090	0.126

D. Pairwise comparisons between the prokaryotic community of the LBFs among the reef areas in each island. Significance codes: 0.05*

	Badi	Padjenekang
	p-value	p-value
Reef flat vs 10m	0.710	0.026*
Reef flat vs 20m	0.412	0.343
10m vs 20m	0.004*	0.001*

E. Pairwise comparisons of the prokaryotic community of the LBFs across reef areas. Significance codes: 0.05*

	A. lessonii	*A. radiata*	*H. depressa*
	p-value	p-value	p-value
Reef flat vs 10m	0.001*	-	-
Reef flat vs 20m	0.001*	-	-
10m vs 20m	0.017*	0.042*	0.043*

ANNEX 5. Seawater and Substrate core microbiome

A. Seawater core microbiome: ESVs found across 90% of all water samples.

ESV	Class	Order
ESV_61	Actinobacteriota	Acidimicrobiia
ESV_65	Actinobacteriota	Acidimicrobiia
ESV_126	Actinobacteriota	Acidimicrobiia
ESV_31	Proteobacteria	Alphaproteobacteria
ESV_43	Proteobacteria	Alphaproteobacteria
ESV_46	Proteobacteria	Alphaproteobacteria
ESV_63	Proteobacteria	Alphaproteobacteria
ESV_66	Proteobacteria	Alphaproteobacteria
ESV_92	Proteobacteria	Alphaproteobacteria
ESV_93	Proteobacteria	Alphaproteobacteria
ESV_100	Proteobacteria	Alphaproteobacteria
ESV_136	Proteobacteria	Alphaproteobacteria
ESV_152	Proteobacteria	Alphaproteobacteria
ESV_161	Proteobacteria	Alphaproteobacteria
ESV_195	Proteobacteria	Alphaproteobacteria
ESV_198	Proteobacteria	Alphaproteobacteria
ESV_235	Proteobacteria	Alphaproteobacteria
ESV_301	Proteobacteria	Alphaproteobacteria
ESV_304	Proteobacteria	Alphaproteobacteria
ESV_307	Proteobacteria	Alphaproteobacteria
ESV_330	Proteobacteria	Alphaproteobacteria
ESV_358	Proteobacteria	Alphaproteobacteria
ESV_374	Proteobacteria	Alphaproteobacteria
ESV_396	Proteobacteria	Alphaproteobacteria
ESV_281	Planctomycetota	Phycisphaerae°
ESV_94	Bacteroidota	Bacteroidia
ESV_97	Bacteroidota	Bacteroidia
ESV_98	Bacteroidota	Bacteroidia
ESV_109	Bacteroidota	Bacteroidia
ESV_166	Bacteroidota	Bacteroidia
ESV_169	Bacteroidota	Bacteroidia
ESV_216	Bacteroidota	Bacteroidia
ESV_247	Bacteroidota	Bacteroidia
ESV_303	Bacteroidota	Bacteroidia
ESV_331	Bacteroidota	Bacteroidia
ESV_342	Bacteroidota	Bacteroidia
ESV_411	Bacteroidota	Bacteroidia
ESV_23	Cyanobacteria	Cyanobacteriia
ESV_51	Cyanobacteria	Cyanobacteriia
ESV_104	Cyanobacteria	Cyanobacteriia
ESV_125	Cyanobacteria	Cyanobacteriia
ESV_91	Proteobacteria	Gammaproteobacteria
ESV_122	Proteobacteria	Gammaproteobacteria
ESV_124	Proteobacteria	Gammaproteobacteria
ESV_153	Proteobacteria	Gammaproteobacteria
ESV_204	Proteobacteria	Gammaproteobacteria
ESV_367	Proteobacteria	Gammaproteobacteria
ESV_400	Proteobacteria	Gammaproteobacteria
ESV_510	Proteobacteria	Gammaproteobacteria

B. Substrate core microbiome: ESVs found across 90% of all substrate samples.

ESV	Class	Order
ESV_21	Proteobacteria	Alphaproteobacteria
ESV_30	Proteobacteria	Alphaproteobacteria
ESV_58	Proteobacteria	Alphaproteobacteria